Cranial muscles of gonorynchiform fishes, with comments on generic relationships

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Introduction

The ostariophysan order, Gonorynchiformes comprises a small group of seven genera, totalling some 30 species of diverse morphology and habitat. Two genera, *Chanos* and *Gonorynchus* are marine and have their distribution in the coastal and shelf waters of the Indo-Pacific. The other five genera, *Kneria, Parakneria, Cromeria, Phractolaemus* and *Grasseichthys* are confined to the freshwaters of Africa. Apart from *Chanos* (see Schuster, 1960), life-history and ecological data are almost entirely lacking.

Only incidental observations are available on *Gonorynchus,* which according to Marshall (1964) feeds on crustacea by burrowing into sand. Such few data as exist on the African freshwater genera *Kneria* and *Parakneria* indicate that they are inhabitants of quiet forest pools as well as fast flowing water areas such as rapids and waterfalls (see Bell-Cross, 1976:96; Nicholson & Nicholson, 1975; Banister & Bailey, 1979:208,214) and are epilithic feeders. *Phractolaemus,* on the other hand, occurs in quiet, shaded waters and may be an epiphytic feeder. Nothing is known of the life-histories of the minute *Grasseichthys* and *Cromeria,* although Roberts (1972:144) reports the latter as spending '. . . much of its time buried in the sand'.

The systematic history of the gonorynchiforms has been summarised by Fink & Fink (1981) and Patterson (1984a). Fink & Fink (1981) provided a positive basis for further systematic research by identifying a suite of synapomorphies, later enumerated and modified by Patterson (1984a & b). In Patterson's (1984a) relationship scheme, the Chanoidei (Chanidae; *Chanos*) are recognised as the sister-group to the Gonorynchoidei, comprising the families Gonorynchidae (*Gonorynchus*), Kneriidae (*Kneria, Parakneria, Cromeria, Grasseichthys*) and Phractolaemidae (*Phractolaemus*). Thus, following Fink & Fink, Patterson recognised the African freshwater taxa as a monophyletic lineage on the basis of five synapomorphies involving the suspensorium, vertebral column and gill-arches.

A re-examination of those primary synapomorphies (i.e. unique to gonorynchiforms within the Ostariophysi) has failed to falisify their status. Similarly, the synapomorphies used to

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unite the Gonorynchoidei are upheld. However, within this suborder, generic relationships amongst the African freshwater taxa are at present unresolved.

Apart from osteology, anatomical studies of gonorynchiforms have dealt with visceral and pulmonary systems (see Thys van den Audenaerde, 1961 on Phractolaemidae and Lenglet, 1973 on the Kneriidae). Virtually no myological data are available for these fishes. The cranial musculature of only one gonorynchoid, *Gonorynchus gonorynchus,* has been described in detail by Le Danois (1966). It is, however, unfortunate that numerous inaccuracies, misidentifications and misinterpretations (see below under *Gonorynchus*) render this work virtually useless.

The aim of this paper is to partly fill the lacunae of descriptive myology and thereby provide another data base for assessing relationships within the Gonorynchiformes. Attention has been directed primarily to those muscles attaching to the jaw, opercular and suspensorial elements as these were thought, because of their more variable nature, to be the most rewarding indicators of phylogenetic relationship. Some of the hyoid muscles and those of the branchial arches are not treated in detail; the pattern of gonorynchiform gill-arch muscles conforms closely to those illustrated for the ostariophysan characiphysan *Brycon* by Winterbottom (1974, figs 20 & 29), apart from the reduced length and tendinous nature of the *levatores externi* in the Phractolaemidae. (Suitable material for examining branchial arch muscles by sectioning was not available for *Cromeria* and *Grasseichthys*.)

Gonorynchiform fishes are not well represented in museum collections, particularly the rarer small-sized African freshwater species. It is fortunate that the British Museum (Natural History) has representatives of all gonorynchiform genera and so it has been possible to make direct osteo-myological comparisons. The opportunity has been taken to comment, where appropriate, on the osteological observations of previous authors.

Abbreviations used in the figures
(Except when given otherwise the scale bar divisions = 1 mm)

Muscles and soft tissues:

a_1 (i, o) a_2 (i, o) a_3, a_w	divisions of *adductor mandibulae* muscle (i = inner, o = outer)	lin	*levator internus*
		lmp	maxillary-palatine ligament
a_2L	lachrymal portion of muscle A_2	lo	*levator operculi*
aa_2	aponeurosis of muscle A_2	lpp	palatine-premaxillaryligament
aap	*adductor arcus palatini*	lq	quadrate spine-quadrate face ligament
ad4	*adductor* of the 4th branchial arch	lri	retroarticular-interopercular ligament
ah	*adductor hyomandibularis*	lrt	coiled upper jaw ligament
ao	*adductor operculi*	mc	maxillary cartilage
b	barbel	nc	nasal cavity transverse canal
bm	body musculature	nt	nasal tube
brp	lateral branchial pouch	od	*obliquus dorsalis*
ca	rictal cartilages	on	olfactory nerve
cmc	coronomeckelian cartilage	pc	palatine cartilage
cms	cartilaginous maxillary-palatine meniscus	ph	*protractor hyoideus*
		pp	*protractor pectoralis*
ctf	fatty connective tissue	pqc	palato-quadrate cartilage
do	*dilatator operculi*	rm	mandibular ramus of the trigeminal nerve
ec	ethmoid cartilage		
ebd	epibranchial diverticulum	rmf	dentary foramen for mandibular nerve
edc	epidermal canal	rs	*rectus superior*
epx	*epaxialis* muscle	sh	*sternohyoideus*
hy	*hyohyoideus*	tA	tendon of muscle A_2o to antorbital
im	*intermandibularis*	ta_1	insertion tendon of muscle A_1
lap	*levator arcus palatini*	ta_2a_1i	tendon from A_2 to A_1 inner muscle
le	*levator externus*	ta_2	insertion tendons of muscle A_2
lep	ethmoid-palatine ligament	ta_2Q	tendon from A_2 aponeurosis to quadrate
li	lower lip	tvd	*transversus dorsalis*

Bones

AA	anguloarticular		N	nasal
AH	anterohyal		OA	opercular aperture
BA4	4th branchial arch		OF	olfactory foramen in the frontal
BB	basibranchial		OP	operculum
BR	branchiostegal ray		P1–4	dentary processes
CB1–5	ceratobranchials		PA	parietal
CM	coronomeckelian bone		PAL	
D	dentary		(A,D)	palatine (auto-, dermo-)
DF	dilatator fossa		PB1–4	pharyngobranchials
EB1–5	epibranchials		PHY	posterohyal
ECT	ectopterygoid		PM	premaxilla
ENT	entopterygoid		PO	preoperculum
EP	epioccipital		PS	parasphenoid
ETH	ethmoid bloc		PTO	pterotic
FR	frontal		PTS	pterosphenoid
HB1–3	hypobranchial		Q	quadrate
HY	hyomandibula		QS	quadrate spine
IO1–5	infraorbitals		RA	retroarticular
IOP	interoperculum		RE	rostrodermethmoid
LAC	lachrymal (1st infraorbital)		SO	subopculum
LE	lateral ethmoid		SP	sphenotic
ME	mesethmoid		SY	symplectic
MET	metapterygoid		UH	urohyal
MX	maxilla		V	vomer

Descriptive myology

Definitions

For the most part, the muscle nomenclature follows that of Winterbottom (1974), including the use of *protractor hyoideus* rather than *geniohyoideus* for the ventral head muscle (see Lauder & Liem, 1980:373 for discussion).

The outer, ventral portion of the *adductor mandibulae* musculature is regarded as division A_1. The definition and homology of this element has been the subject of much discussion (see below, for various authors), and further comments are added below although no solution to the problem is offered.

Winterbottom (1974) defines muscle A_1 as an element having a dorsal position on the cheek musculature and inserting on the maxilla. However, Winterbottom noted that the position and insertion were not constant and thus he recognised A_1 as a muscle of variable topography. Following examples given by Edgeworth (1935:53) Winterbottom considered that because the mandibularis branch of the fifth cranial nerve was variable in its path it could not be taken as a reference point for identifying a particular muscle. I would contest this, however, on the grounds that Edgeworth had probably mistaken the homology of the elements he identified as A_1 (in siluroids for example, Edgeworth's A_1 is the *retractor tentaculi,* which originates from the medial face of the adductor complex; see Howes, 1983a:11 for discussion of homology). Furthermore, nerves do not alter their courses randomly but become displaced according to the shift of the muscle element with which they are associated (see below, p. 299 and Howes, 1983b:328).

By defining A_1 as the element inserting on the maxilla and lying *exterior* to mandibular V, a more precise identification may be possible. On this basis the ventral, outer element in ostariophysans is clearly A_1. In elopoids (*Elops*), alepocephalids (*Alepocephalus*), clupeids (*Clupea*) and most 'salmoniforms' (*Salmo, Coregonus, Esox*), even though the outer muscle element may have a maxillary insertion, it is clearly not A_1 since the mandibular V lies external to it. Furthermore, the outer element in these groups most often inserts on the lower jaw and is continuous with an intramandibularis section (A_w) and so must be considered A_2 ($+A_3$), as identified by Winterbottom (1974:figs 1 & 2).
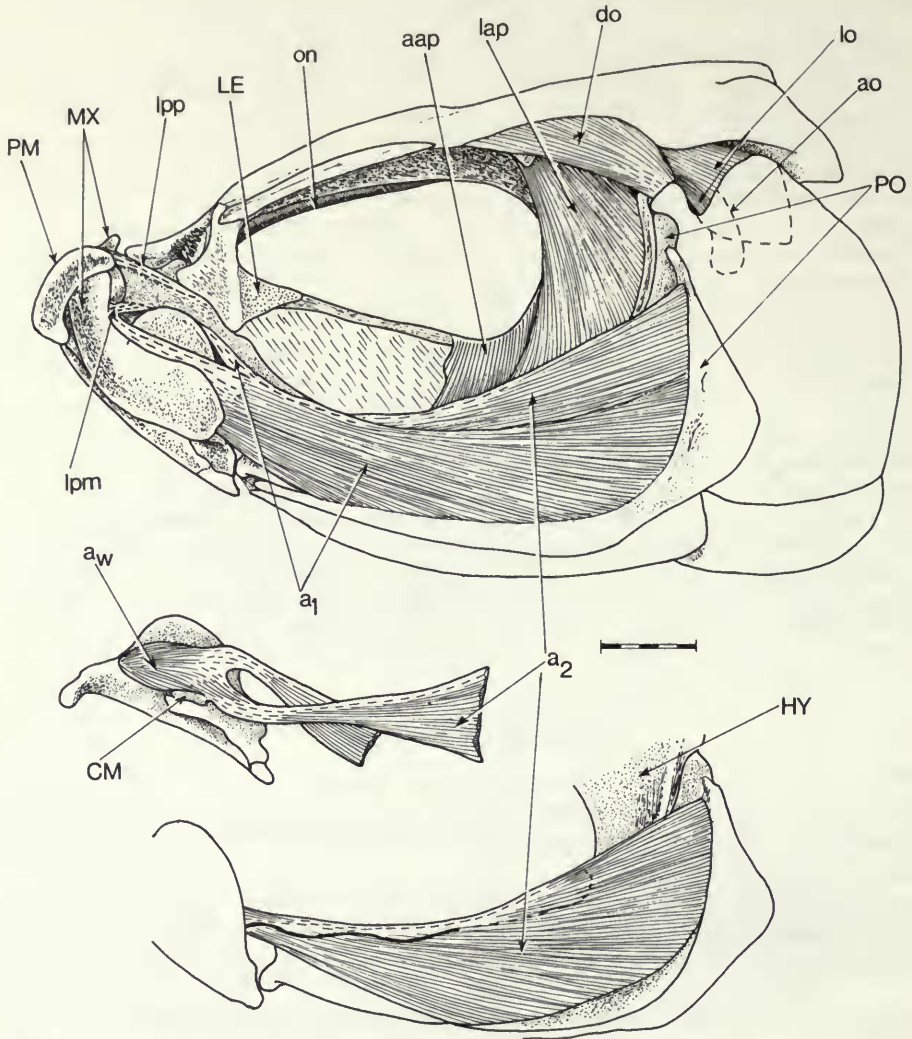
Fig. 1 *Chanos chanos*. Above: lateral view of cranial muscles. Dashed lines on operculum indicate the extent of the *levator* and *adductor operculares* insertions. Centre: medial view of lower jaw muscle insertions. Below: lateral view of inner adductor muscle; dashed line indicates medial path of the mandibularis nerve, shown in solid black laterally.

In Gadiformes (*Gadus, Melanogrammus, Nezumia*), the mandibular ramus of V lies medial to A_1 and external to A_2. In Stomiiformes (*Astronesthes*), the mandibular ramus passes lateral to the outer adductor element, but there is an insertion to the upper jaw of a medial division of the adductor, often referred to as A_1b. Fink & Weitzman (1982:72) have argued that A_1 and A_1b are not homologues. I agree with this conclusion, but the problem still remains whether muscle A_1 in neoteleosts is equivalent to A_1 in ostariophysans. Fink & Weitzman (1982:72) claim that A_1 is a 'eurypterygian character' (i.e. is present in groups above and including Aulopiformes). This statement suggests that their concept of A_1 differs from that given here, since by regarding the muscle as characterising eurypterygians they exclude ostariophysans. It is noted that these authors refer to A_1 as a *dorso*-lateral division of the adductor mandibulae.

Amongst some 'salmoniforms' *viz*: *Galaxias, Prototroctes, Brachygalaxias* and *Aplochiton* there is a partial ventro-lateral division of the *adductor mandibulae* and the mandibularis V nerve
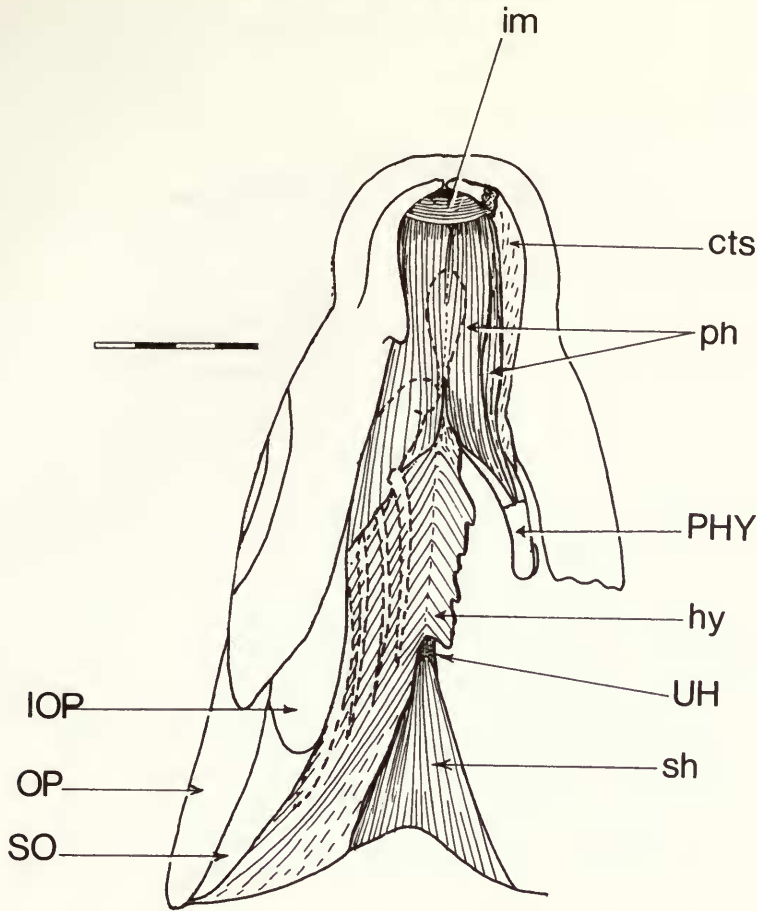
Fig. 2 *Chanos chanos*. Ventral head musculature. Outlines of hyoid elements are indicated by dashed lines.

passes lateral to A_2. The nerve courses across the inner muscle close to its insertion tendon and passes into the body of the outer element. In other words, these taxa possess a muscle segment topographically identical with that defined as A_1 in ostariophysans. Whether indeed it is homologous or homoplasious is a matter that needs further investigation.

One other problem must be mentioned, and this concerns the plesiomorphic nature of insertion of muscle A_1 in ostariophysans. Fink & Fink (1981:343) contended that a maxillary insertion of the element is plesiomorphic. Howes (1983a:14) argued the reverse, believing that a lower jaw insertion was the primitive condition. No conclusive evidence has emerged from the present study that would support either one or other of these hypotheses; either assumption of primitiveness recognises a reversal if one acknowledges each ostariophysan subgroup as being monophyletic.

CHANOS Lacepède, 1803

Chanos is a monotypic genus represented by *Chanos chanos* (Forsskål, 1775) found in tropical and subtropical areas of the Indian and Pacific oceans. The species inhabits mainly coastal, and often brackish waters and is an epipelic feeder.

SPECIMENS EXAMINED: *Chanos chanos*: BMNH 1948.10.15:1–2 (185, 220, 290 mm SL); uncatalogued (8 alcian-alizarin preparations, 23–47 mm SL); 1898.9.13:1 (dry skeleton, neurocranial length 70 mm).
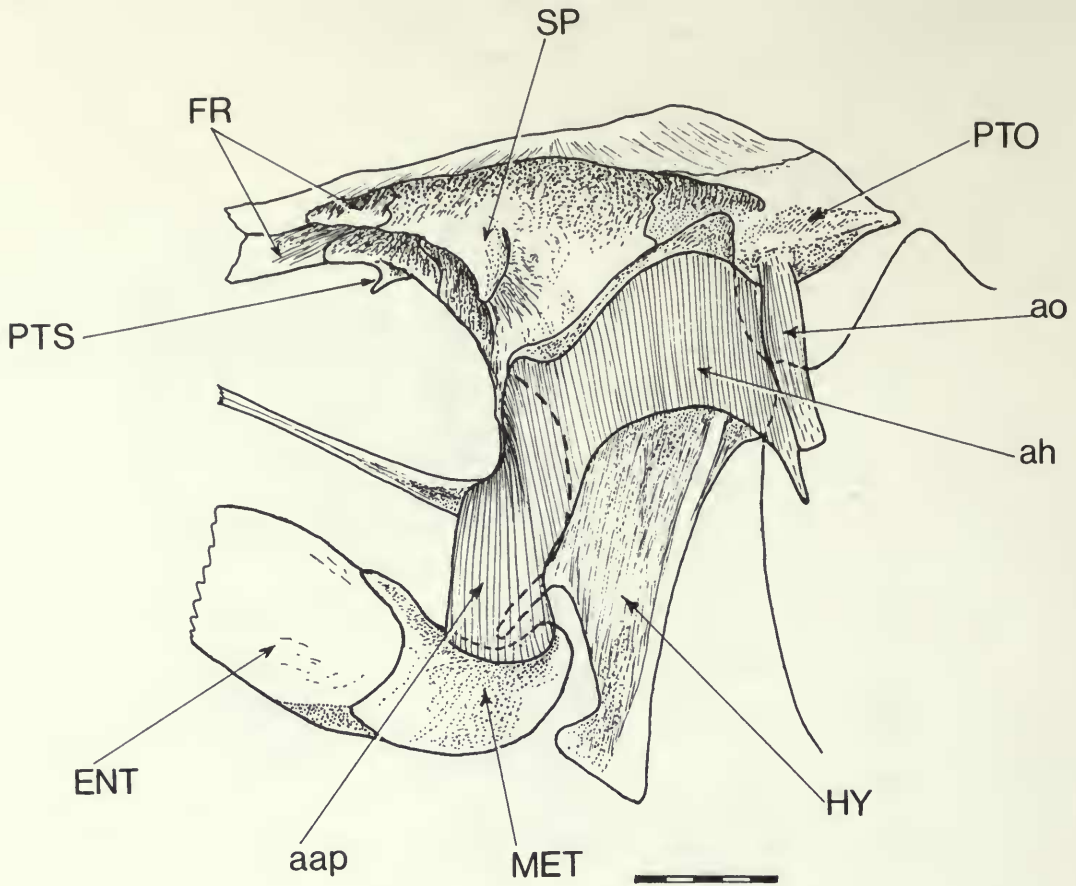
Fig. 3 *Chanos chanos.* Lateral view of suspensorial musculature. Dashed lines indicate *overlying* bony elements.

Muscles attaching to the jaws (Figs 1–3). The *adductor mandibulae* is a thin, elongate muscle with a markedly concave, tendinous orbital border; its origin is from the skin covering the cheek, the face of the preoperculum, the posterior border of the hyomandibular and the posterior extension of the quadrate. Posterodorsally the muscle is divided, the inner element, A_2, inserting *via* a long and deep tendon on to the coronomeckelian bone in the lower jaw. A slip of fibres branches dorsally from A_2 tendon to become continuous with the fibres of the intramandibularis division of the muscle (A_w).

The outer element, A_1, has a double insertion, the outer fibres terminating *via* a deep tendon on the connective tissue fascia of the medial face of the maxilla, at its midpoint; another tendon branches off from the dorsal face of the muscle to join an aponeurosis from which extends A_w. Prior to its branching this tendon is tightly bound to the quadrate by connective tissue.

The *protractor hyoideus* (Fig. 2) is a thick, wide element running from the dorso-, ventral- and anterohyals of each side. Laterally, a narrow bundle of fibres detaches from the main element and has a separate, tendinous attachment to the anterohyal. Anteriorly, at the midpoint of the lower jaw, the *protractor* divides, each segment inserting on its respective dentary at the point of that bone's greatest curvature. A thin, wide *intermandibularis* muscle joins the mandibles, having its points of attachment above and below those of the arms of the *protractor hyoidei*.

Suspensorial and opercular muscles (Figs 1 & 3). The *levator arcus palatini* is a large pyramidal muscle extending between the sphenotic and lateral face of the hyomandibula. The *adductor*

arcus palatini is a large, bolster-like element confined to the posterior portion of the parasphenoid and its ascending process. Insertion is on the metapterygoid. There is a distinct division between the *adductor arcus palatini* and the *adductor hyomandibularis,* the latter muscle extending from the upper part of the prootic to the dorsal, medial face of the hyomandibula. Posteriorly, the *adductor hyomandibularis* inserts on the operculum together with fibres of the *levator operculi.* The *dilatator operculi* occupies a deep cranial fossa comprising the frontal, sphenotic and pterotic bones, the sphenotic being the major contributor. The fossa is roofed by the frontal, although the sphenotic process and its associated part of the dilatator muscle project laterally from beneath the frontal roof.

There are two sections of the *levator operculi,* one stemming from the pterotic border, the other from the slightly recessed ventral surface of the pterotic. Both sections insert together over a triangular area of the medial face of the operculum. The *adductor operculi* originates anteriorly and somewhat medially to the *levator* and has its insertion anteroventral to that muscle.

Comments

Chanos has a double insertion of muscle A_1, to the upper and lower jaws. In *Albula,* a muscle identified as A_1b by Greenwood (1977:71) inserts both on the maxilla and joins the aponeurosis of A_w. However, as discussed above (p. 275) this element would not seem to be homologous with A_1 in *Chanos* since it lies medial to the mandibularis ramus of nerve V.

Other anatomical features. Features of the ethmoid region of *Chanos* were commented upon and figured by Fink & Fink (1981). My observations on double-stained specimens agree for the most part with their figures. I would disagree, however, with their interpretation of the cartilaginous body lying between the palatine and ethmoid. According to Fink & Fink (1981) this is an ethmo-palatine cartilage. In none of the specimens I have examined does this nodule contact, or closely approach the ethmoid cartilage (cms Fig. 4) and, indeed in Fink & Fink's figure (1981, fig. 3A), there is no contact between these elements. Furthermore, whereas Fink & Fink show the element with convex faces I find that in all the specimens to hand, it is a thin disc with markedly concave faces (Fig. 4). In fact, the element has the appearance of a simple meniscus between the cartilaginous medial process of the maxilla and the palatine cartilage.
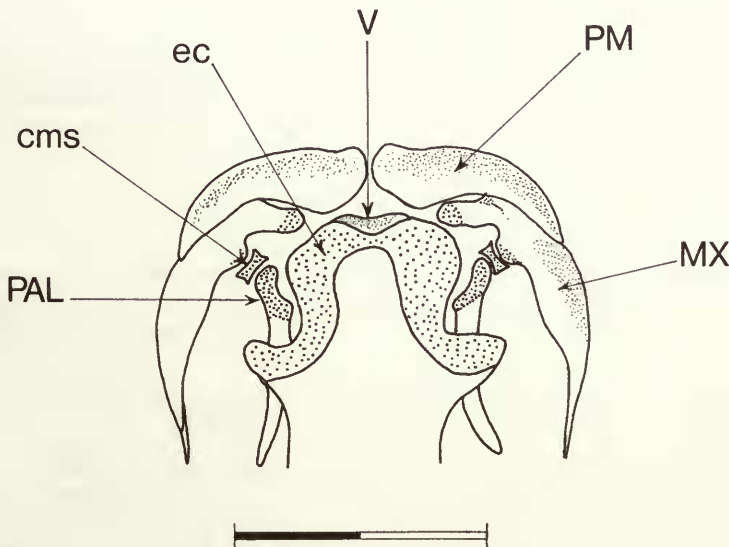

Fig. 4 *Chanos chanos.* Dorsal view of ethmoid region of a specimen 45 mm SL.
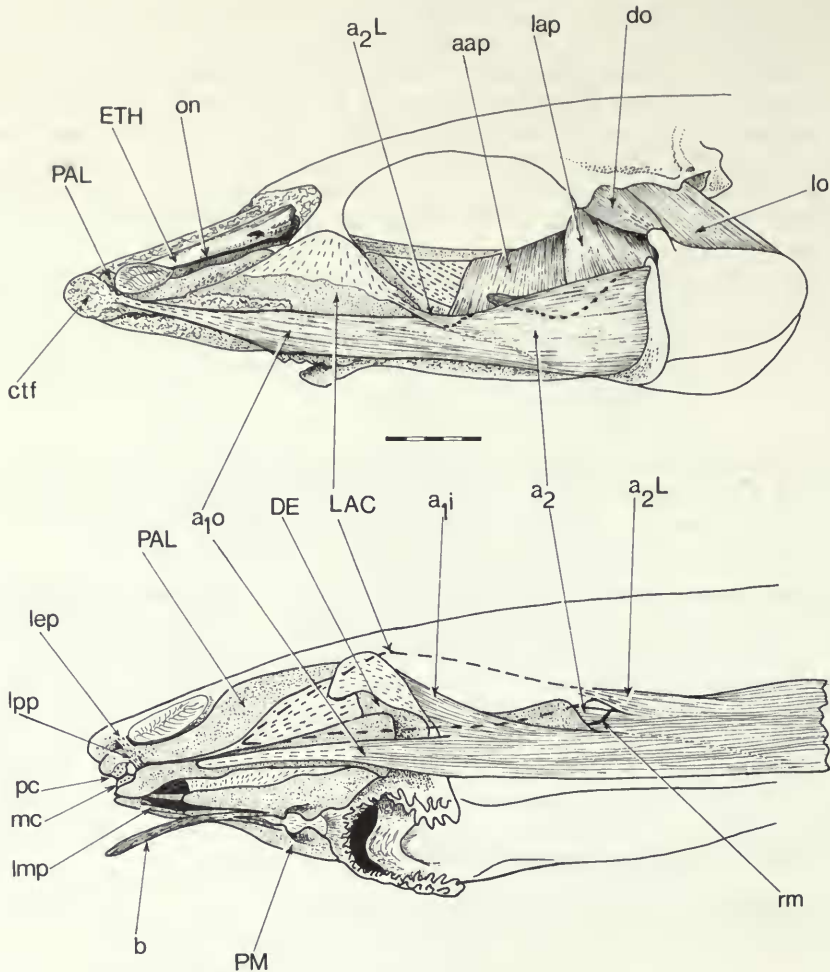
Fig. 5 *Gonorynchus gonorynchus*. Upper: lateral view of cranial muscles. Heavy dashed lines indicates medial path of mandibularis nerve. Lower: ventro-lateral view of jaw musculature lachrymal bone is indicated by dashed outline.

GONORYNCHUS Scopoli, 1777

According to Fowler (1936) and Nelson (1984:122) there is probably only a single species *G. gonorynchus* (Linn., 1766) having an Indo-Pacific and southern Atlantic continental shelf distribution. However, Ferraris (pers. comm.) has evidence to suggest that there are seven species.

SPECIMENS EXAMINED: *Gonorynchus gonorynchus* Uncat. 203 & 290 mm SL; 1914.2.18:25 (alizarin prep.); *G. greyi* 1875.11.12:27; 1885.3.3:16 (both dry skulls), 1914.8.20.34 (204 mm SL).

Muscles attaching to the jaws (Figs 5–7). Superficially there appears to be a single, elongate muscle originating from the preoperculum; about halfway along a medial portion separates from the main bundle to insert, principally, on the lower jaw. Its points of insertion, and the position of the mandibularis nerve, which is interlaced within its fibres, suggest that the element is A_2. The outer part of the muscle continues forward to insert on the upper and lower jaws and is designated as A_1.
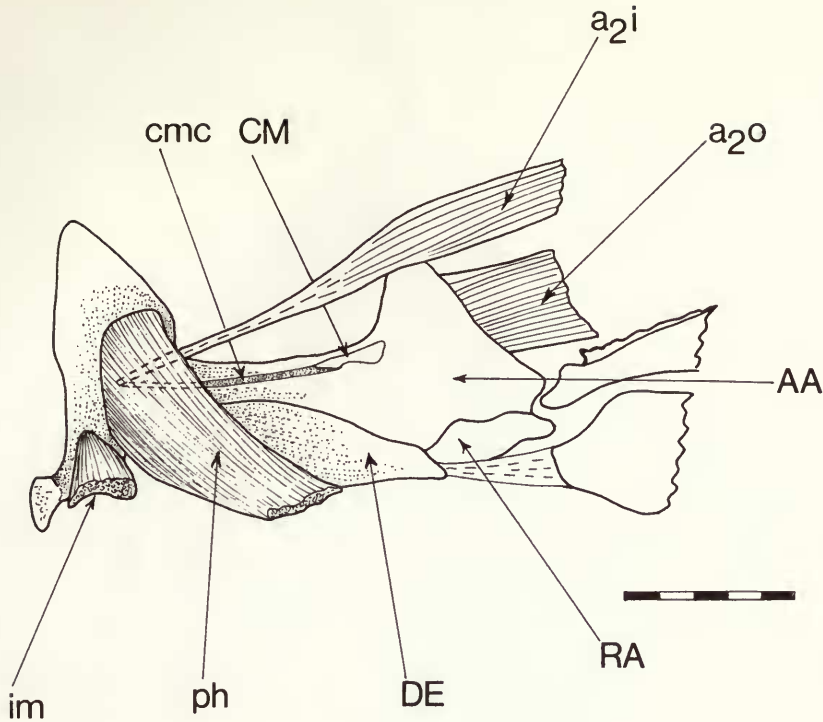
Fig. 6 *Gonorynchus gonorynchus*. Medial view of lower jaw muscle attachments.

Muscle A_1 separates from the main adductor mass at a point posterior to the coronoid process of the dentary; a broad medial bundle of fibres inserts into the thick connective tissue surrounding the coronoid process (a_1o, Fig. 5), whilst the outer, elongate segment runs forward to insert via a narrow tendon about half-way along the maxilla (a_1i, Fig. 5).

Muscle A_2 has three insertions (Figs 5 & 6); 1, an outer (a_2o), to the rim of the anguloarticular; 2, an inner (a_2i) *via* a long tendon to the anterior tip of the coronomeckelian cartilage; 3, a lateral (a_2L) to the posterior tip of the lachrymal. There is no intramandibularis (A_w) section of the adductor muscle.

The *protractor hyoideus* (Figs 6 & 7) stems from each hyoid bar, the two halves joining at an aponeurosis below the anterohyals and extending forward joined in the midline by connective tissue fascia. Anteriorly, the halves separate, diverge dorsally and insert on their respective dentaries at a point almost level with the rim of the coronoid process (Fig. 6).

Laterally, the *protractor hyoidei* are firmly attached to tendinous connective tissue that extends upward to line the inner side of the suspensoria. A large *intermandibularis* muscle connects the two dentaries and lies anteroventral to the insertion of the *protractor hyoidei*.

Suspensorial and opercular muscles (Figs 5 & 8). The *adductor arcus palatini* is a well-developed muscle originating from the prootic and the posterior part of the parasphenoid, its ventral insertion is on the quadrate and the dorsal margin of the preoperculum. A medial bundle of fibres inserts on the rod-like metapterygoid. Where the *adductor* joins the preoperculum, a long segment of fibres separates off from the body of the muscle to attach to the sclerotic covering of the eyeball. Ventro-posteriorly, the fibres of the *adductor* intergrade with those of the *levator arcus palatini*. A posterior portion of the *adductor* stems from the pterotic and inserts on the medial face of the hyomandibula; this segment is considered to be the *adductor hyomandibularis*.
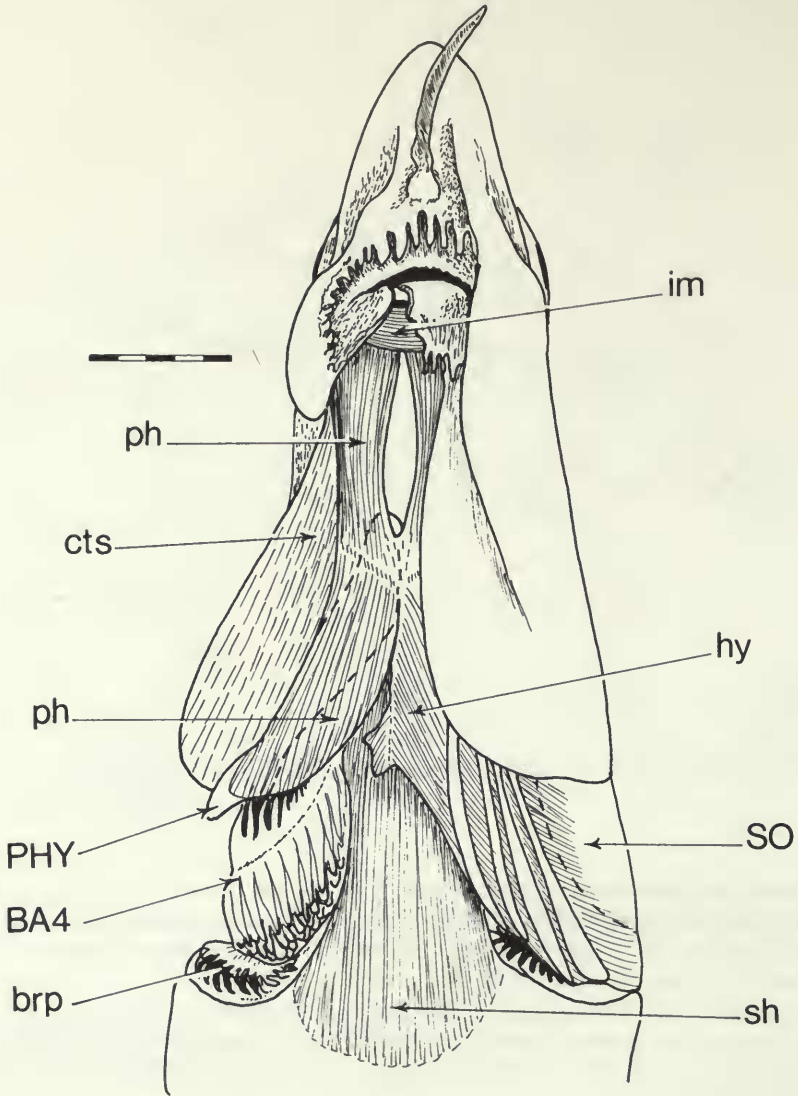
Fig. 7 *Gonorynchus gonorynchus*. Ventral head musculature. Outlines of hyoid and opercular elements indicated by dashed lines. The *protractor hyoidei* have been pulled apart in the midline.

The *levator arcus palatini* extends from the sphenotic process to insert on the lower half of the hyomandibula and the upright limb of the preoperculum. At its origin, the fibres are continuous with those of the *dilatator operculi*.

The dilatator operculi originates partly from the posterior rim of the sphenotic process and partly from a shallow sphenotic-pterotic fossa. Insertion is on the long anterior process of the operculum. The *levator operculi* has two origins, an outer one from the deeply concave posterior face of the hyomandibula and an inner one from that area of the pterotic medial to the hyomandibular fossa. At this site, the fibres of the *levator operculi* are contiguous with those of the *adductor hyomandibularis*. The *levator* inserts along the upper medial face of the operculum. The *adductor operculi* is a cone-shaped muscle originating posterior to the hyomandibular fossa, and inserting on the postero-medial area of the operculum.
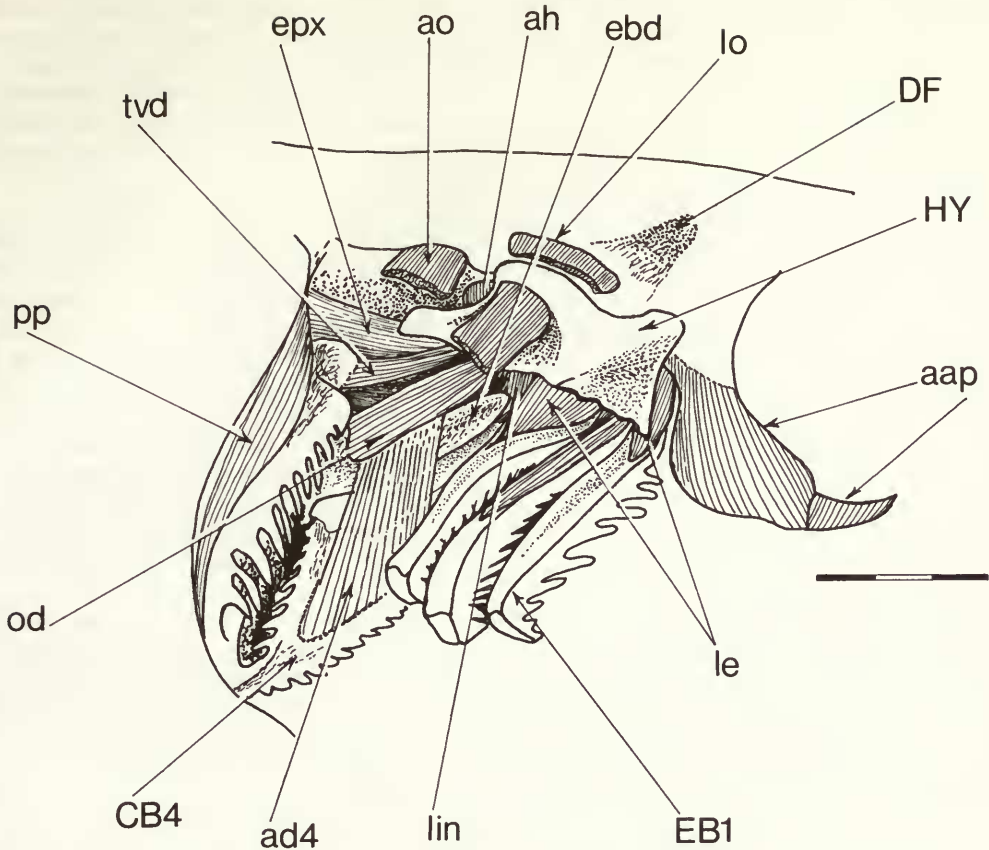
Fig. 8 *Gonorynchus gonorynchus*. Suspensorial, opercular and branchial arch musculature. The opercular muscles and hyomandibula have been cut through to expose the upper gill-arch muscles. The small ventral segment of the aap inserts on the eyeball covering.

Comments

Le Danois (1963; 1966) described the jaw and hyoid musculature of *Gonorynchus*. However, her descriptions and those presented above have few points in common. It would be unproductive to detail every difference between my interpretation and that of Le Danois of *Gonorynchus* musculature; the following examples are the most disparate.

Le Danois (1966) recognises three distinct divisions of the adductor musculature, labelled as 'muscle preorbitaire externe', 'A$_1$' and 'muscle quadrato-mandibulare interne'. These correspond respectively to my A$_1$ outer, A$_1$ inner and A$_2$ divisions. Several muscles she illustrates such as 'muscle labial sous cutane', 'muscles labio-rostraux' and 'labio-premaxillaire' simply do not exist in any specimens I have examined and I can only conclude that Le Danois has mistaken the thick, fibrous connective tissue occurring in those areas as muscle fibres.

Compared with other ostariophysans the jaw and suspensorial muscles of *Gonorynchus* display certain derived features. As in *Chanos,* muscle A$_1$ has a double insertion with part of the muscle inserting on the lower jaw (? a plesiomorphy). Muscle A$_2$ has a tripartite insertion, with an outer segment inserting on to the lachrymal. The insertion of the *protractor hyoideus* high on the dentary coronoid process is an autapomorphic feature. The quadrate and preopercular attachments of the *adductor arcus palatini* are possibly unique amongst ostariophysans. Absence of A$_w$ is a feature shared with other gonorynchoids.

Other anatomical features. *Jaw bones and their ligaments:* The premaxillae are long triangular bones lying almost horizontally (Fig. 5). In shape and alignment they are strongly reminiscent of the premaxillae of some notacanthids (see Greenwood, 1977). Each premaxilla is attached to its respective maxilla by a ligament extending from its anterior tip. A ligament attaches the tip of the maxilla to the palatine. The maxillary tip also articulates with a ventral cartilaginous process of the palatine *via* a cartilaginous meniscus (as in *Chanos*). The single, symphysial barbel is connected to each premaxilla by a bifurcated ligament.

Nasal sac: Derscheid (1924:160) described the nasal sac in *Gonorynchus,* but due to paucity of material was unable to delimit '. . . the shape, the extent and the relationships' of the caudal extremity of the sac. According to Gosline (1961:28), the nasal sac extends '. . . back in the flesh external to the large lacrimal'. This is an error; the area above the lachrymal is covered with dense fatty tissue and no portion of the sac intrudes there. Monod (1963) although in disagreement with Gosline (1961) regarding the lateral position of the sac, was none the less of the opinion that the terminal caecum of the sac extended well posteriorly and may even be linked to a 'muscle particulier'. In fact, the nasal sac, whilst relatively large, has no peculiar feature. It lies above the palatine and is bordered ventro-posteriorly by the lachrymal and dorsally by the nasal bone. The thick olfactory nerve courses inward, alongside the borders of the vomer and parasphenoid, passing through a frontal foramen, lying above the lateral ethmoid, and thence into the cranial cavity (Fig. 9). Thus, the notable feature concerning the gonorynchid nasal organ is the frontal foramen through which the olfactory nerve passes, and which must be regarded as an autapomorphy for the genus.

Ethmo-vomerine region (Fig. 10): Some comments seem appropriate on the peculiar nature of the ethmoid and vomer which appears to have escaped the attention of previous authors. The dorsal surface of the ethmoid (? rostrodermethmoid) is seen as somewhat spatulate with a semi-circular anterior border. Underlying it is a tube-like central portion (mesethmoid) the opening of which is exposed anterior to the ethmoid border. The anterior, lamellate border of the mesethmoid has a medial notch. The elongate vomer terminates anteriorly beneath the tubular portion of the mesethmoid.

Infraorbital bones (Fig. 10): The anterior circumorbital bone was identified by Woodward (1896:503) and Ridewood (1905:364) as a preorbital and by Gosline (1961:28) as a lachrymal. Monod (1963:258) discussed the identification of the bone and concluded that it was '. . . en fait, quadripartite', illustrating it as an antorbital overlying a series of three infraorbitals.

In alizarin stained preparations it is clear that there are a total of five infraorbitals, *contra* Ridewood (1905) who claimed infraorbitals were lacking. The 1st infraorbital (lachrymal) is a large, triangular, lamellate bone with a narrow canal along its ventral border containing two or three ventrally facing pores. The bony canal is preceded by a short epidermal canal opening terminally at the tip of the snout (Fig. 10). The posterior portion of the lachrymal canal overlies the anterior part of the 2nd infraorbital, which, like the remainder of the infraorbitals, is reduced to the bony sensory canal; the third is sometimes fragmented (Fig. 10).

Gill arches (Fig. 9): Monod (1963, fig. 40) shows the 4th epibranchial comprised of two portions, a cartilaginous element separated by a space from the epibranchial proper. I find no such separation, the 4th epibranchial having a noticeable cartilaginous process apposing the tip of the bow-like 5th epibranchial.

The 4th gill-arch is served by a particularly well-developed *adductores* muscle (ad4, Fig. 8) which attaches to a fascia extending from the *obliquus dorsalis* (elevateurs internes 5 of Le Danois, 1966:313, fig. 18).

Le Danois (1966:313, fig. 25) erroneously refers to, and illustrates the median part of the epaxialis muscle as a *retractor dorsalis*. Her justification for so naming the muscle is its attachment to the pharyngeal tooth plate. Pharyngeal tooth plates are absent in *Gonorynchus,* and the extension of the muscle to what appears to be a 'metapterygoid' tooth patch in her figure is non-existent.

Other derived features such as the lateral and median buccal cavity processes and pectoral and pelvic fin appendages do not occur in other gonorynchiforms and are considered as autapomorphies for *Gonorynchus* (see Le Danois, 1966 and Monod, 1963 for descriptions).
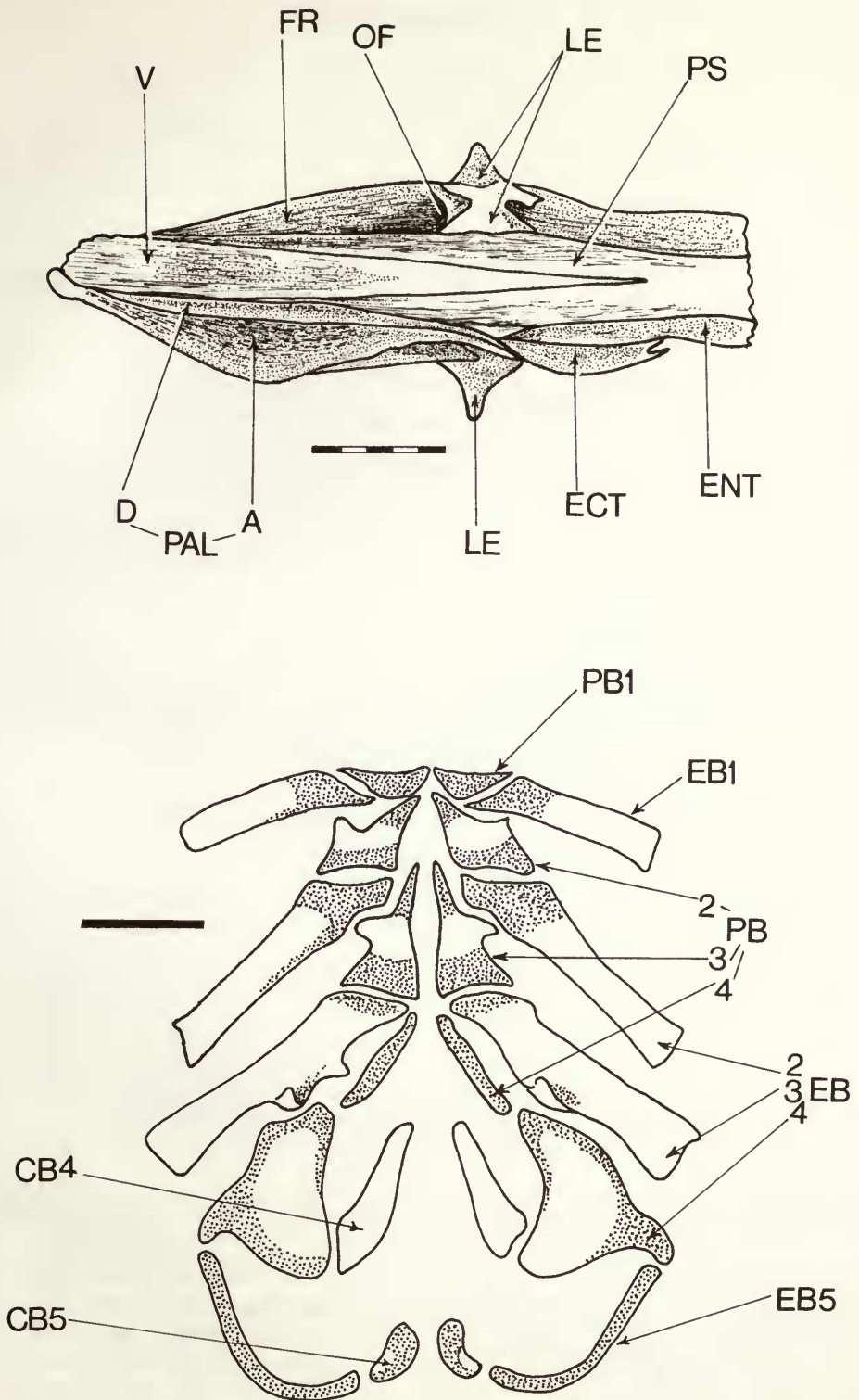
Fig. 9 *Gonorynchus gonorynchus.* Above: ventral view of anterior region of neurocranium and suspensorium. Below: dorsal view of branchial arch elements. Of the lower elements, only ceratobranchials 4 and 5 are shown.
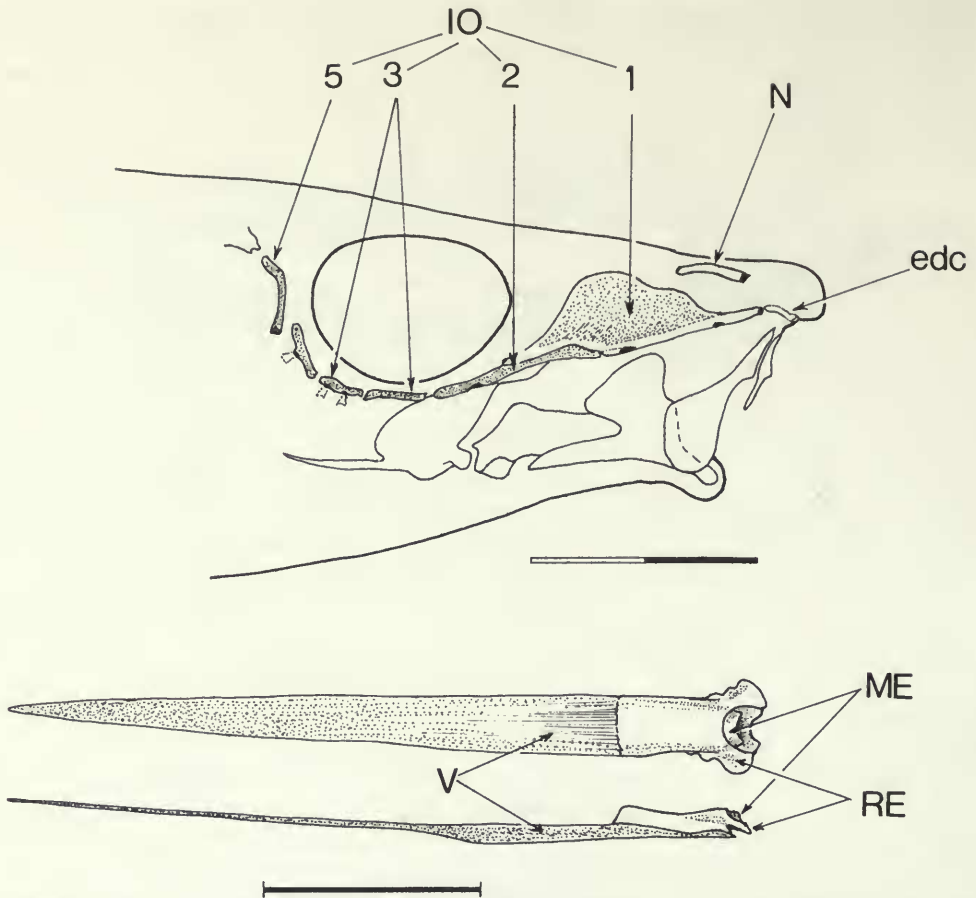
Fig. 10 *Gonorynchus gonorynchus*. Above: lateral view of head showing infraorbital bones and jaw elements. Below: dorsal and lateral views of ethmo-vomerine elements.

KNERIA Steindachner, 1866

PARAKNERIA Poll, 1965

These two genera are considered together since their myology is virtually identical (see remarks on p. 299 concerning generic status). There are *ca* 24 species in both genera combined, distributed in east, west and central Africa (see Poll, 1965 and Roberts, 1975 for detailed distributions).

SPECIMENS EXAMINED: *Kneria auriculata* BMNH 1967.5.2:1–4;8–15; *K. katangae* 1976.10.20:116–137; *K. wittei* 1976.10.20:142–160; 1953.1.26:1–6 (alizarin preps); uncatalogued (alcian-alizarin prep.); *Parakneria tanzaniae* 1976.10.21:163–172 (including alizarin specimen).

Muscles attaching to the jaws (Figs 11–12). The *adductor mandibulae* comprises three distinct elements; 1, an outer cone-shaped muscle (a_1o, Fig. 11) originating from the horizontal limb of the preoperculum and inserting on the medial face of the broadly expanded maxilla (the maxilla lies in an almost transverse plane and so its medial face is positioned posteriorly); 2, a short, stout muscle (a_1i, Fig. 11) originating from the leading edge of the quadrate and extending dorso-laterally at an angle of 45° to insert on the inner face of the maxilla, medial to A_1o; 3, an inner muscle (a_2, Fig. 11) originating from the preoperculum and running virtually horizontally with insertion *via* a long tendon on to the coronomeckelian bone. There is no intramandibularis section (A_w) of the adductor.
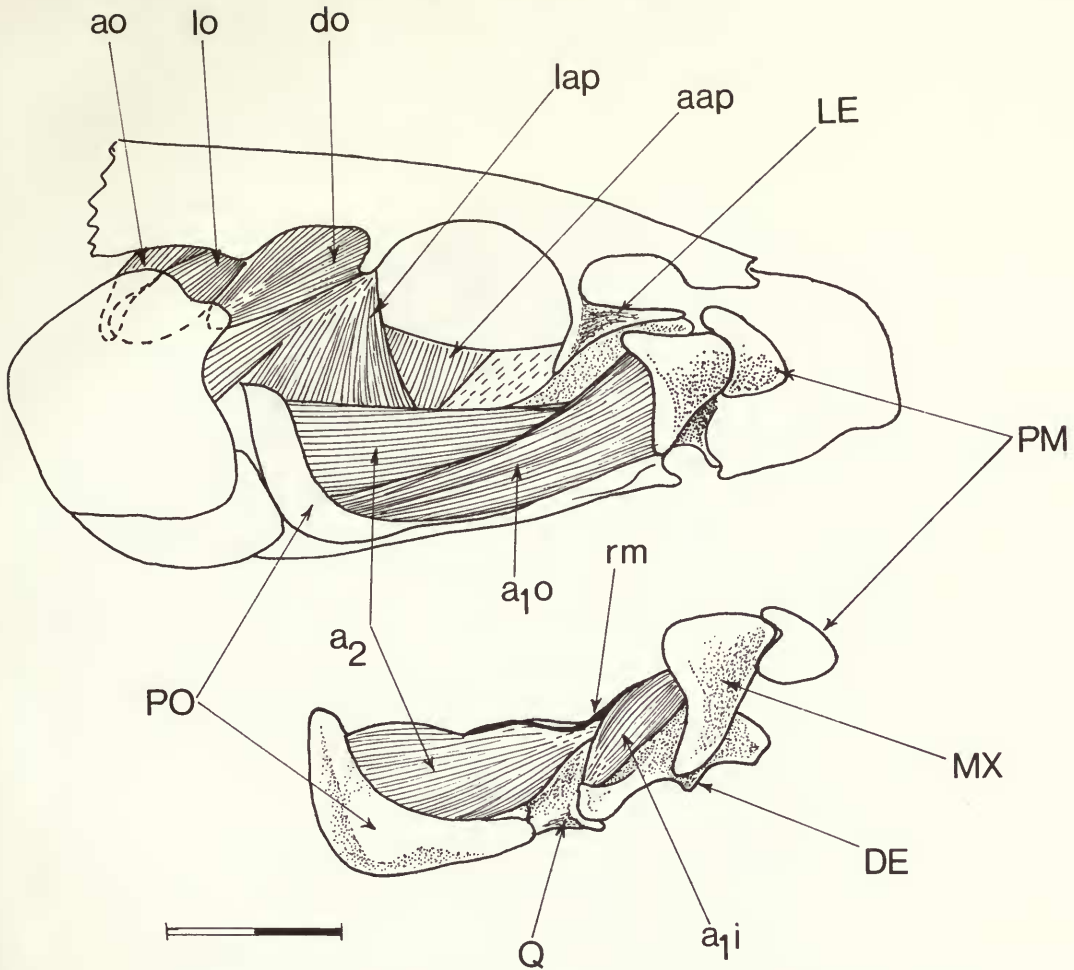
Fig. 11 *Parakneria tanzaniae*. Above: lateral view of cranial muscles. Below: lateral view of inner jaw muscles.

Each portion of the *protractor hyoideus* (Fig. 12) extends from its respective hyoid bar to meet its antimere in the midline prior to separating, diverging and inserting on to the ventral process of the dentary (P3, Fig. 13). the *intermandibularis* connects the anterior portions of the divergent dentaries and passes above the protractor hyoideus.

Suspensorial and opercular muscles. The *adductor arcus palatini* runs from the posterior part of the parasphenoid and inserts along the entire medial face of the hyomandibula. The *levator arcus palatini* originates from the sphenotic process and inserts on the borders of the hyomandibula and operculum.

The *dilatator operculi* extends from a rudimentary sphenotic fossa to the dilatator process of the operculum. The *levator* and *adductor operculares* originate respectively from the pterotic fossa, their overlapping insertions being on the upper medial face of the operculum.

Comments

The jaw muscles of *Kneria* and *Parakneria* display a derived state in that the inner element of A_1 has its origin from the quadrate border and runs obliquely lateral. Such a feature has not been
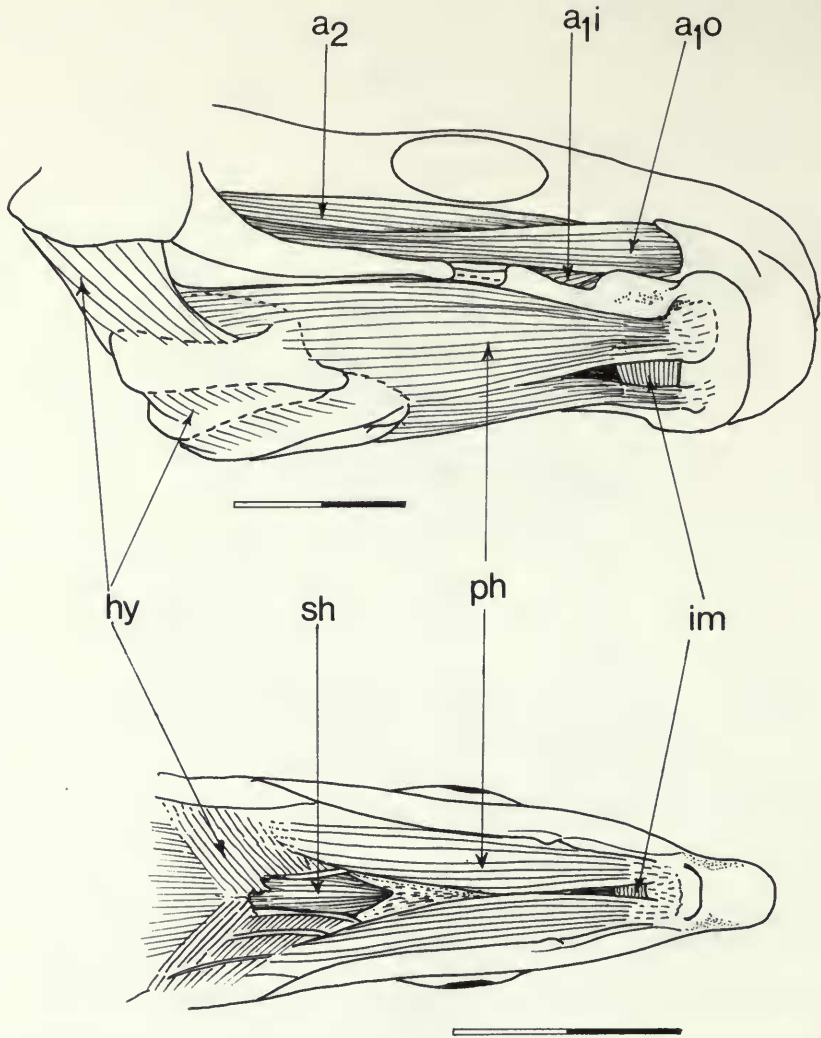
Fig. 12 Ventral head of muscles of: above, *Parakneria tanzaniae*; below, *Cromeria nilotica*.

reported in other ostariophysans and appears similarly only in *Cromeria* (see below) and in a more derived form in *Phractolaemus* (see below).

Other anatomical features: *Lower jaw* (Fig. 13). The lower jaw is complex and was not adequately described in Lenglet's (1974) treatment of kneriid osteology. In both *Kneria* and *Parakneria* the dentary curves laterally at almost a right angle; its lateral flange is notched medially and produced into a process (P3) on to which the *protractor hyoideus* inserts.

Because of the outward curvature of the dentary, the coronoid process has a posteriorly concave face which bears two processes, one lateral (P1) and one medial (P4). These processes provide insertion points for, respectively, muscles A_1o and A_1i. A broad shelf-like process (P2) extends posteriorly and this cups the anterior tip of muscle A_1o. The coronomeckelian protrudes above the dorsal margin of the dentary (see also Lenglet, 1974, figs 12 & 13) and provides the point of insertion for muscle A_2. *Ethmo-vomerine region* (Fig. 14). The vomer in *Kneria* and *Parakneria* extends beyond the ethmoid bloc and its head is inclined ventrad at a sharp angle.
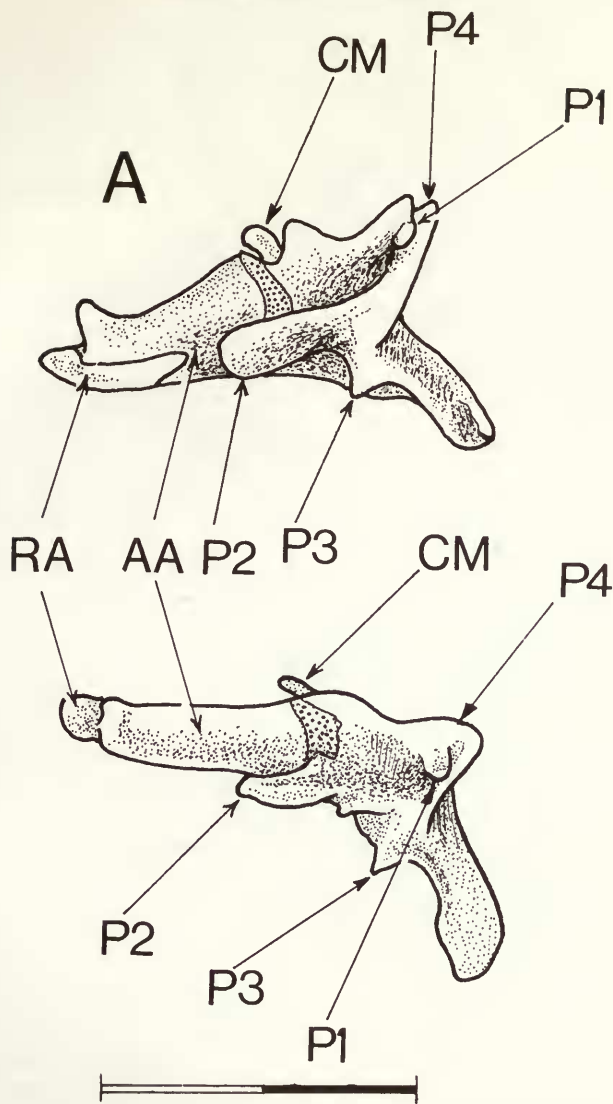
Fig. 13 *Kneria wittei.* Lower jaw in lateral (above) and dorsal (below) views.

The vomer is joined synchondrally to the overlying mesethmoid which bears a short rostral process and spatulate wings. The lateral ethmoid curves forward sharply and extends anteriorly (Fig. 11) and is covered laterally by the antorbital. *Pterosphenoids* (Fig. 14). Lenglet (1974) stated that pterosphenoids are absent in kneriids. They are, however, present, and like those of other gonorynchiforms are small and widely separated.

CROMERIA Boulenger, 1901

A monotypic genus represented by *C. niloticus* Blgr, 1901 from the Nile, Niger, Volta and Tchad basin.

SPECIMENS EXAMINED: BMNH 1969.11.14:124–135 (including 4 alcian-alizarin preparations).
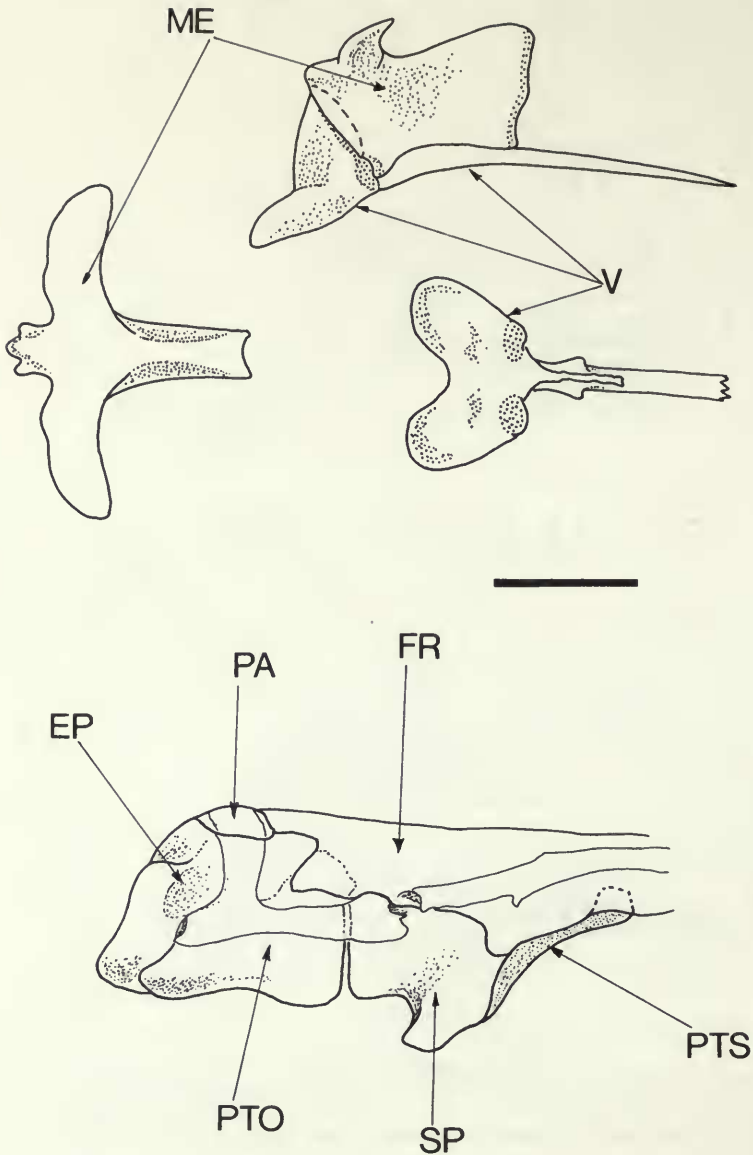
Fig. 14 *Parakneria tanzaniae*. Above: ethmo-vomerine region in lateral view; dorsal views of mesethmoid (left) and vomer (right). Below: lateral view of the upper bones of the cranial wall. Scale = 0·5 mm.

Muscles attaching to the jaws (Figs 16 & 12). The *adductor mandibulae* comprises 1, an elongate, horizontal muscle, A_1o which originates from the preoperculum and quadrate and inserts *via* a broad tendon on to the maxilla and the connective tissue covering the upper jaw bones; 2, a medial muscle, A_1i that originates from the leading edge of the quadrate, runs somewhat laterally, and inserts on the rim of the maxilla; and 3, muscle A_2 which originates from the preoperculum. Below the centre of the orbit A_2 becomes aponeurotically constricted and linked to the quadrate by a tendinous band which runs mesad from the aponeurosis. From the point of
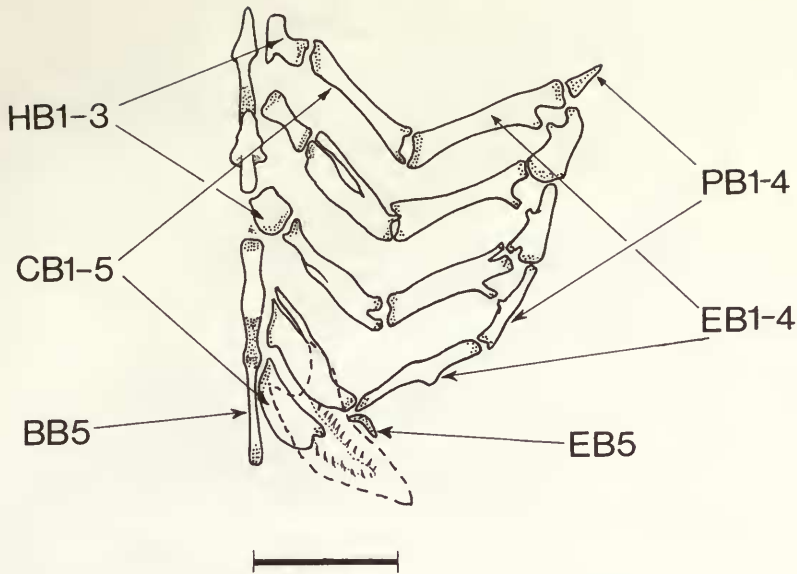
Fig. 15 *Kneria wittei.* Branchial arch elements (right side). Dashed lines indicate extent of epibranchial diverticulum; gill-rakers are also indicated.

its constriction to its insertion, the muscle is represented by a tendinous sheet which fans out to form tripartite attachments with the palatine, the coronomeckelian (see d'Aubenton, 1961:148), and the connective tissue covering the medial face of the maxilla. There is no intramandibularis (A_w) section of the *adductor mandibulae.*

Each part of the *protractor hyoideus* extends from its respective hyoid bar to meet its antimere in the plane of the lower jaw articulation (Fig. 12). Anteriorly, the halves of the muscle diverge to insert into a tendinous sheet extending along the length of the lower jaw. The *intermandibularis* runs dorsad to the *protractor hyoideus,* attaching beneath a medial flange on each dentary.

Suspensorial and opercular muscles (Fig. 16). The *levator arcus palatini* originates from the sphenotic and inserts across the lower, anteriorly extended, portion of the hyomandibula. The *dilatator operculi* is barely discernible from the *levator arcus palatini* as a separate muscle since their fibres are contiguous at their sphenotic origin. Insertion in on the dilatator process of the operculum. The posterior suspensorial muscle appears to be an *adductor hyomandibularis* since it originates from the prootic and pterotic. The anterior fibres run on to the fascia of the suspensorium, whilst the posterior, and majority, of its fibres insert on the dorso-medial face of the hyomandiubla. The *levator operculi* is an extensive muscle, stemming from the pterotic and inserting along the medial edge of the long opercular border. The tubular *adductor operculi* also originates from the pterotic and inserts on to the medial face of the operculum below that of the *levator.*

Comments

The configuration of the jaw muscles most closely resembles that of *Kneria* and *Parakneria,* both in the almost horizontal arrangement of muscle A_1 and in the presence of a medial muscle A_1i having its origin from the quadrate border. The *levator operculi* is more extensive than in *Kneria* and *Parakneria* and indeed, most closely resembles that of *Gonorynchus,* except that in the latter genus the *levator operculi* also has its origin from the hyomandibula.

In *Cromeria* the opercular margin is sealed to the body wall leaving only a small ventral opening above the pectoral fin base. The posterior opercular borders of *Kneria, Parakneria* and
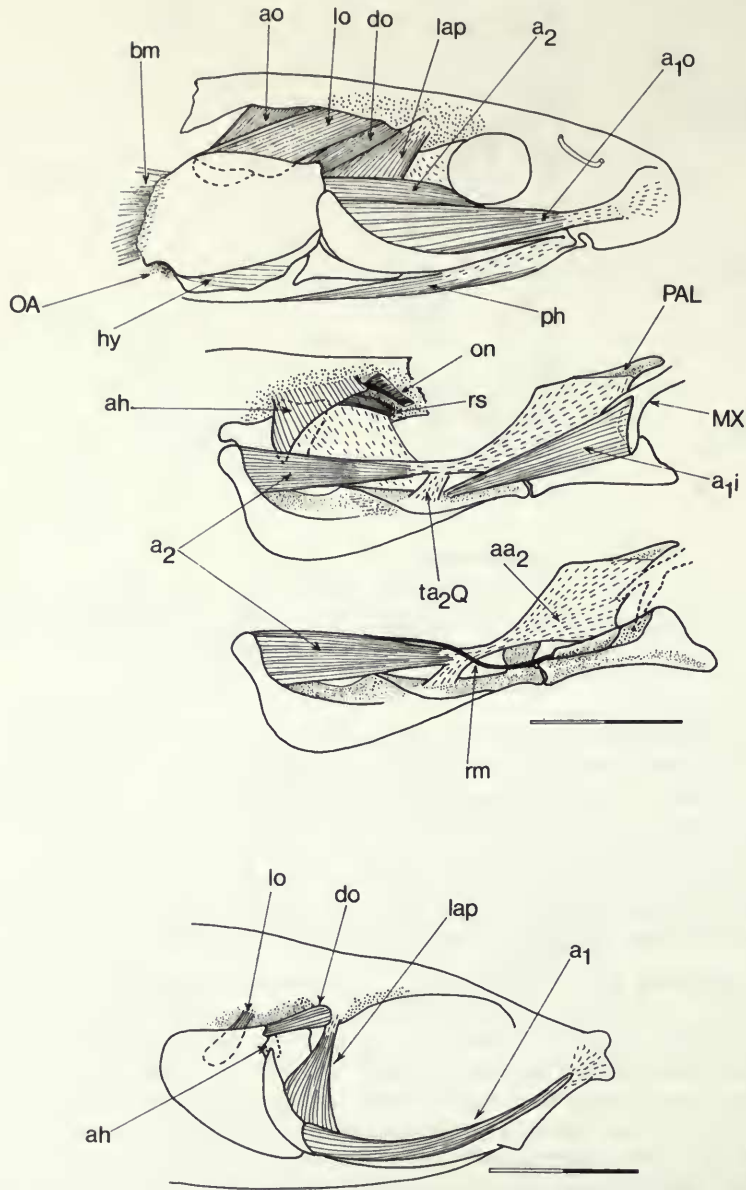
Fig. 16 *Cromeria nilotica* (above), three lateral views showing cranial and superficial jaw muscles; inner jaw and suspensorial muscles (dashed line indicates *overlying* hyomandibula) and innermost jaw muscle and its tendinous connections.

Grasseichthys gabonensis (below), lateral view of cranial muscles. The *adductor hyomandibularis* is shown in outline by a closely-dashed line.

Grasseichthys (see below) are partially sealed, that of *Grasseichthys* having a condition midway between *Cromeria* and the kneriid genera. In *Phractolaemus* only the dorsal border of the operculum is sealed to the body wall.

Other anatomical features: *Ethmoid region* (Figs 17A & B). The osteology of *Cromeria* has been adequately dealt with by Swinnerton (1903) and d'Aubenton (1961). It is clear from these works
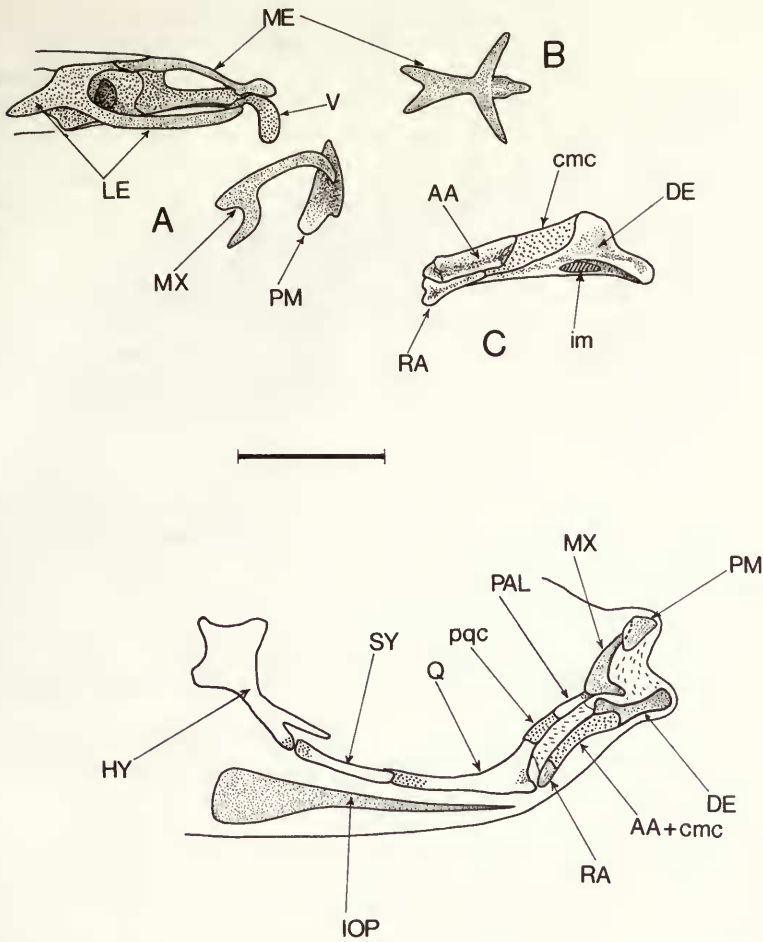
Fig. 17 Above: A, *Cromeria nilotica,* lateral view of ethmoid region and medial view of upper jaw; B, dorsal view of mesethmoid; C, medial view of lower jaw. Below: *Grasseichthys gabonensis,* lateral view of jaw and suspensorial bones.

and personal observations that four derived features are shared with *Kneria* and *Parakneria,* namely, the rostral extension and ventral inclination of the vomer, the long mesethmoid lateral wings, and the anterior curvature and anterior extension of the lateral ethmoids. In specimens examined the curvature of the lateral ethmoids is so great that their anterior tips fall in the same transverse plane as that of the mesethmoid lateral wings. (Fig. 17A).

GRASSEICHTHYS Géry, 1964

A monotypic genus represented by *G. gabonensis* Géry, 1964, from the Ivindo basin, Gabon, and the cuvette centrale, Zaire (see Roberts, 1972:134).

SPECIMENS EXAMINED: BMNH 1966.10.20:1–10; 1984.9.12:62 (alcian-alizarin preparation).

Muscles attaching to the jaws (Fig. 16). There is a single adductor muscle (?A_1) comprised of a narrow band of fibres, originating laterally from the inner face of the infraorbital series and posteriorly from the lower limb of the preoperculum. Insertion of the muscle is tendinously to the connective tissue investing the rictus of the jaws, with the majority of fibres appearing to

insert into the tissue covering the maxilla. There is, apparently, no inner muscle (A_2) or intramandibularis, (A_w) attaching to the lower jaw (but see below with regard to A_2).

The *protractor hyoideus* is thin and narrow, resembling that of *Cromeria*; each segment inserts *via* a narrow tendon on to its respective dentary. The *intermandibularis* is a mere layer of fibres passing between the dentaries above the *protractor hyoideus*.

Suspensorial and opercular muscles. The *levator arcus palatini* is a thin, band-like element originating from the sphenotic. Its fibres run almost vertically to their insertion on the preoperculum. The *dilatator operculi* originates from the postero-ventral portion of the sphenotic, a typical dilatator fossa being absent. The *adductor operculi* is a thin, tubular element inserting mid-dorsally on the medial face of the operculum. I am unable to ascertain the presence of an *adductor arcus palatini* or a *levator operculi* in the material to hand. However, the *levator* is possibly such a thin element that it has been destroyed in removing the connective tissue layer. There is a small *adductor hyomandibularis* running from the prootic to the postero-medial face of the hyomandibula.

Comments

The jaw and suspensorial muscles of *Grasseichthys* are greatly reduced in comparison with those of other gonorynchiforms and indeed, most teleosts. The *adductor mandibulae* is reduced to a mere slip of fibres which would seem to activate, principally, the upper jaw, but whose insertions are not at all definite. Neither is it definite that this muscle represents A_1; it could, conceivably, be homologous with the dorsal branch of A_2 in *Phractolaemus* (see below) which also attaches to the rictal tissue covering the upper jaw. Unfortunately, I am unable to trace the path of the mandibularis V nerve in the specimen available, the course of which would establish the identity of the element.

The lower jaw, which is merely a slender curved rod with a slight coronoid process (Fig. 17), would thus seem to be adducted passively *via* a connective tissue-ligamentous linkage with the lower.

Other anatomical features. The mesethmoid bears a rostral process and long lateral wings and greatly resembles that of *Cromeria*. The lateral ethmoid, however, lacks the anteriorly directed lateral processes present in other kneriids. No ectopterygoid could be detected in the specimen examined. *Grasseichthys* has an elongate, spine-like interoperculum (Fig. 17), a feature shared with *Phractolaemus* (see p. 297).

PHRACTOLAEMUS Boulenger, 1901

A monotypic genus represented by *P. ansorgei* Blgr, 1901. Two subspecies are recognised (see Thys van den Audenaerde, 1961:113, *P. a. ansorgei* Blgr, 1901 from the Niger drainage and *P. a. spinosus* Pellegrin, 1925 from the central Zaire basin.

Specimens examined: BMNH 1979.3.5:217–219 (104 & 110 mm SL); 1984.9.27:3–12 (130,120, 120 mm SL, 115 mm SL alizarin prep.).

Muscles attaching to the jaws (Figs 18–21). The lateral cheek muscles are readily distinguished as two elongate elements. The ventral muscle (A_1) narrows into a thin tendon as it approaches the jaw articulation; the tendon passes beneath a bridge formed by a short, thick ligament attached from the outer quadrate spine to the lateral face of the quadrate (1q), and across the base of muscle a_1i (see below). Exiting from the bridge, the tendon turns through 90° whereupon it joins a broad aponeurosis from which extend two muscle segments. The ventral segment (a_1o, Figs 16 & 18) is a thin sheet of fibres, a bundle of which inserts on the distal cavity of the maxilla (Fig. 19B), whilst the remainder cover the rictal cartilages that lie ventrally and between the dentaries and insert on the connective tissue extending between the maxilla and the small premaxilla.

The dorsal segment (a_1i, Figs 18 & 19A & B) of the muscle originates ventrally from the quadrate spine, covers the outer face of the lower jaw and inserts on the posterior process of the curved maxilla.
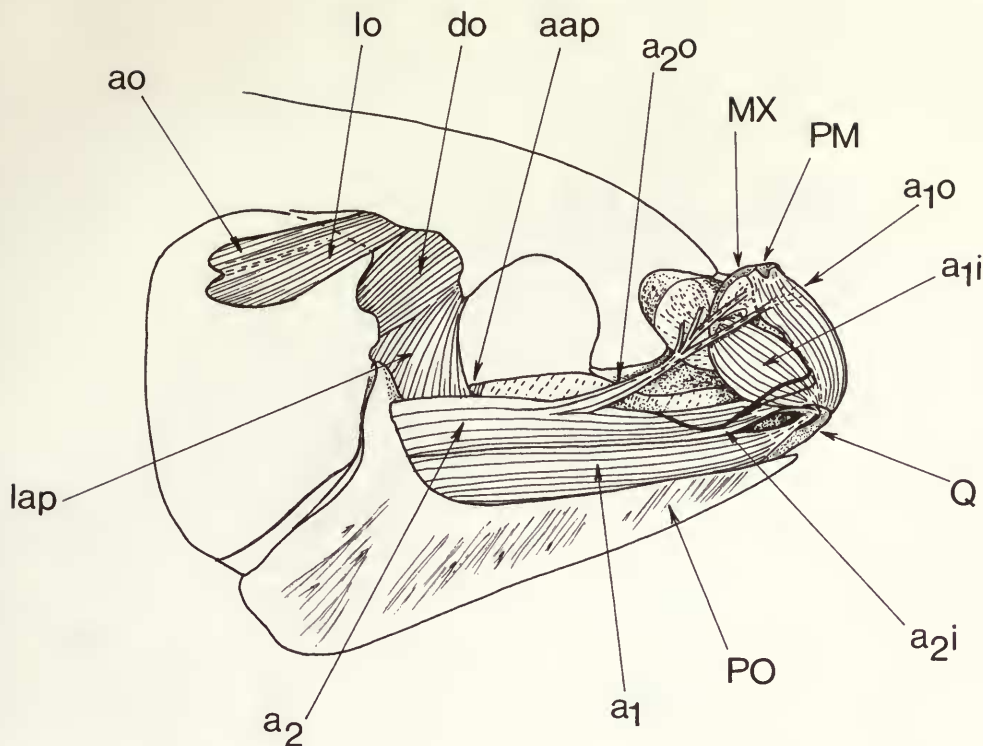
Fig. 18 *Phractolaemus ansorgei*. Lateral view of cranial muscles.

The dorsal adductor muscle (A_2) originates from the preoperculum and hyomandibula. Below the lateral ethmoid a segment of fibres (a_2o, Figs 18 & 19A) branches off from the main body of the muscle and inserts *via* two long, dorsal and ventral, tendons into the connective tissue covering the rictal cartilages. At least three small tendons branch off from the long dorsal tendon and insert on the innner face of the antorbital. The body of A_2 (a_2i, Fig. 19C) continues forward, its insertion tendon divides, the inner inserting on the coronomeckelian bone, and the outer branch making an aponeurotic connection with element A_1i. There is no intramandibularis (A_w) section of the *adductor mandibulae*.

Each part of the *protractor hyoideus* extends forward from the hyoid bar to meet its antimere along a median raphe (Fig. 20). At the jaw articulation each half separates and inclines dorsad to insert *via* its respective tendon on to the anguloarticular. The insertion point of the *protractor* is ventral to the origin of the *intermandibularis,* which, contrary to the known condition in other teleosts, runs between the anguloarticulars rather than the dentaries (Fig. 21).

Suspensorial and opercular muscles. The *levator arcus palatini* originates from the sphenotic and inserts on the broad anterior extension of the hyomandibula. The *adductor arcus palatini* and *adductor hyomandibularis* are contiguous, the anterior part of the muscle (*aap*) originating from the posterior portion of the parasphenoid and the prootic. Insertion is on the dorsal rim of the metapterygoid. The posterior part of the muscle originates from the prootic and pterotic and inserts on the hyomandibular medial face.

The *levator operculi* extends from the junction of the pterotic-prootic with some dorsal fibres stemming from the connective tissue surrounding the *adductor hyomandibularis*; insertion is on the anterior inner face of the operculum. The *adductor operculi* originates from the posterior region of the pterotic and joins the *levator* along a medial aponeurosis, both muscles insert on to
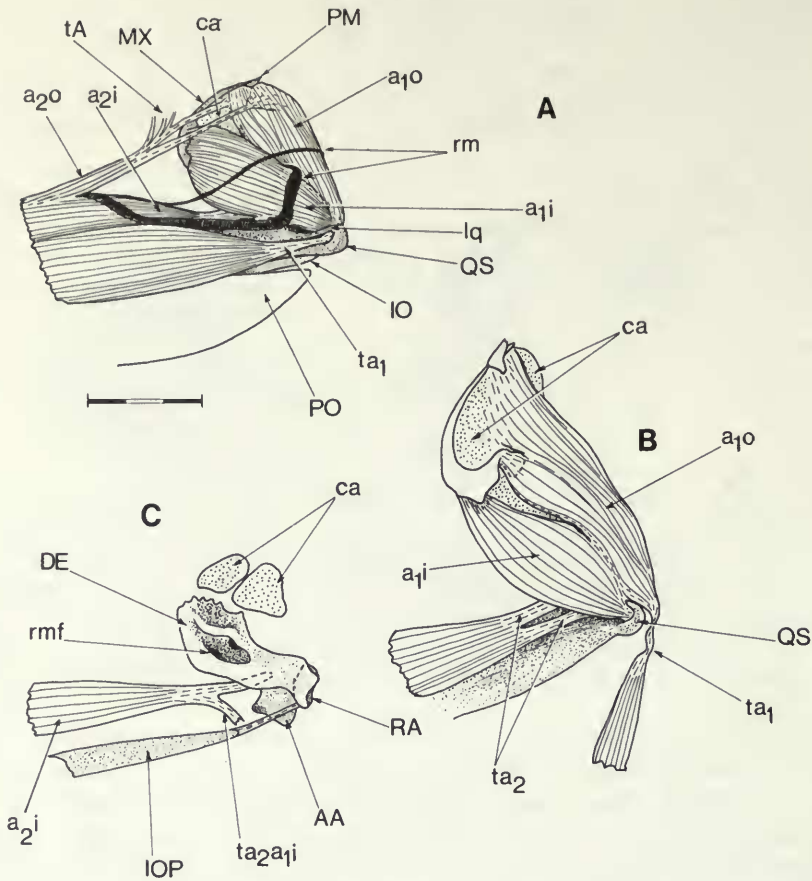
Fig. 19   *Phractolaemus ansorgei.* Anterior jaw musculature in: A, lateral view; B, dorso-lateral view, muscle A_1 has been cut posteriorly and moved laterally to the quadrate spine to expose the lower portion of A_1i; the ligament joining the quadrate spine to the quadrate face (1q) has been removed, as has muscle A_2o; C, lateral view of the lower jaw with the various parts of A_1 and A_2o removed. The upper tendon (dashed line) of A_1i inserts on the coronomeckelian bone.

the concave medial face of the operculum above the levator ledge. The *dilatator operculi* originates from the sphenotic process and pterotic ventral border, there being no dilatator fossa; the muscle inserts on the thick anterior process of the operculum.

Comments

Phractolaemus resembles other non-chanoid gonorynchiforms in the elongate, almost tubular adductor musculature. The curious arrangement of muscle A_1 with its anterior division is reckoned to be the counterpart of the situation in *Kneria, Parakneria* and *Cromeria* (see above). As in those taxa, the dorso-anterior element in *Phractolaemus* originates from the quadrate and inserts on the posterior margin of the maxilla. *Phractolaemus* shares with *Cromeria* a divided insertion tendon of muscle A_2, one segment of which runs to the quadrate origin of muscle A_1i.

   Both Géry (1962) and Thys van den Audenaerde (1961) describe the possible mechanism of jaw protrusion in *Phractolaemus*. Poll (1957) and Géry (1962) figure the snout in a protruded position, it appearing proboscis-like with the mouth rotated from its dorsal, retracted position to a ventral feeding position. The mechanics of jaw adduction and abduction cannot be readily ascertained from the morbid anatomy and any functional hypotheses are beyond the scope of
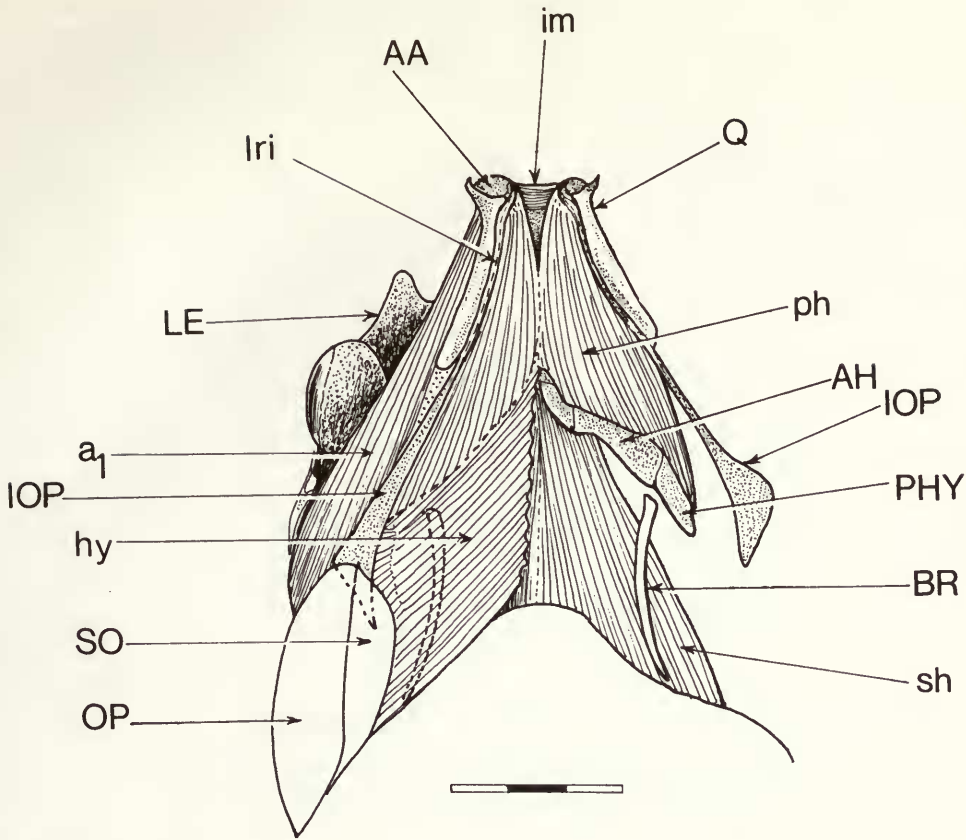
Fig. 20 *Phractolaemus ansorgei*. Ventral head musculature. The *hyohyoideus* is cut away from the specimen's left side to expose the hyoid bar and the single branchiostegal ray; the left interoperculum has been separated from the *hyohyoideus* and hyoid bar to which it is tightly bound.

this work. However, Sara Fink has pointed out to me that a mandibulohyoid ligament is apparently absent in *Phractolaemus* and that the hyoid bar is tightly bound to the interoperculum; observations with which I concur. In this case the abduction mechanism involving the *sternohyoideus* acting *via* the hyoid and mandibulohyoid ligament (Lauder, 1982) is absent. The extensive (?elastin) X-shaped ligaments attached to the upper jaws (ligament pseudocartilagineaux of Thys van den Audenaerde, 1961) seemingly recoil against the protruding vomer (lrt, Fig. 21) and muscle A_2, the outer section of whose tendinous insertions run to the antorbital and skin covering the underside of the lower jaw, must be considerably tensed during jaw abduction and exert a strong contracting force. The unique shift of the *intermandibularis* from the anterior to the posterior regions of the jaws is concomittant with the development of the circular, tube-like mouth involving symphysial separation of the dentaries.

Other anatomical features. Thys van den Audenaerde (1961) described the anatomy (minus the myology) of *Phractolaemus ansorgei* and drew attention to its many peculiarities. Amongst the osteological features are the excessively broad frontals; deep infraorbitals; extensive development of the preopercular bones which overlap in the ventral midline; reduced suspensorial elements, including absence of a symplectic, and an elongate spine-like interoperculum. The vomer is an almost square bone with an anterior notch; it projects anteriorly from beneath the mesethmoid, its anterior border curving upward. To the vomer is attached the central ligament (see above),
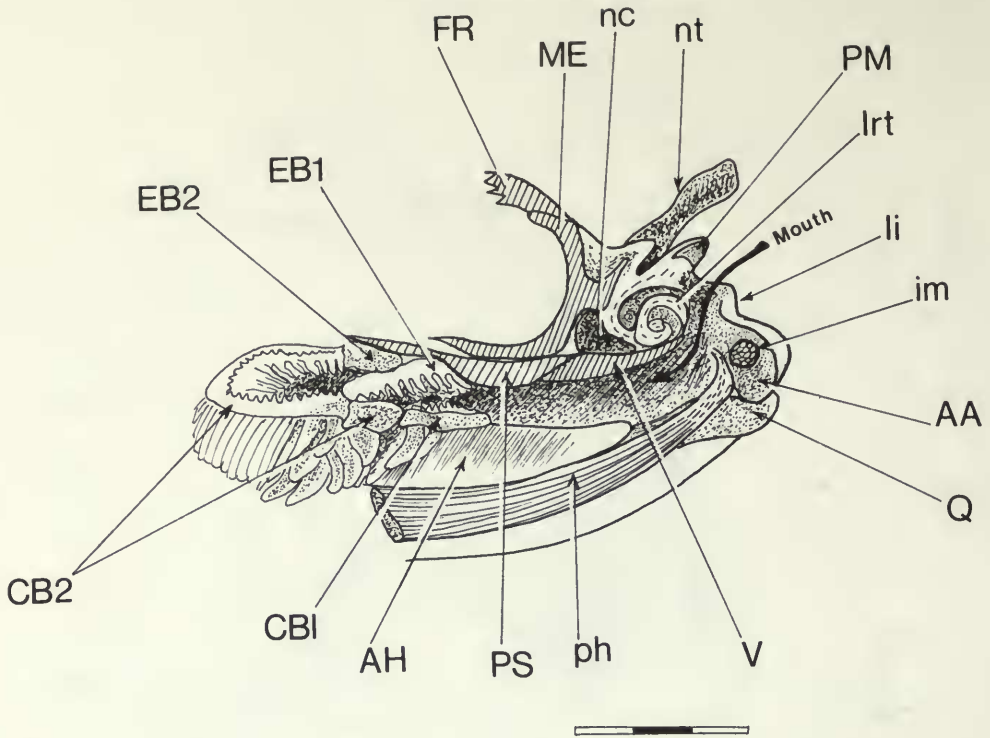
Fig. 21 *Phractolaemus ansorgei.* Sagittal section through the anterior cranium and buccal cavity. The branchial arches and hyoid bar are those of the left side.

from which branches extend laterally to the palatines and anteriorly to the maxillae (see Thys van den Audenaerde, 1961, Fig. 19). When the ligament is recoiled it lies on the vomerine shelf and in this sense resembles the coiled kinethmoid ligament of some cyprinoids. The vomer also floors a transverse canal, backed and partially roofed by the mesethmoid (nc Fig. 21), that connects the nasal tubes. The nasal bone lies at the medial base of the tube.

The statement in Nelson (1984:123) that *Phractolaemus* possesses teeth is erroneous.

Discussion

The hope of a conclusive pattern of relationships of the gonorynchid genera emerging from an anlaysis of jaw and suspensorial muscles has not been realised. Most of the taxa display many autapomorphic myological features and their resemblances are symplesiomorphic. Nevertheless a few specific points can be made.

Adductor musculature

Muscle A_1 is present in all gonorynchiforms, and in all genera, apart from *Chanos,* is an elongate, almost tubular element. The muscle has a double insertion in all genera, although the insertion points are variable; in *Chanos* and *Gonorynchus* part of A_1 inserts on the lower jaw whereas in *Kneria, Parakneria, Cromeria* and *Phractolaemus* A_1 is completely divided, the inner section derived in whole or part from the anterior border of the quadrate. In the kneriid genera the mandibularis ramus of nerve V runs medial to and along the dorsal border of the inner segment

of muscle A_1 (a_1i). In *Phractolaemus,* when the jaw is adducted, the nerve crosses the lower face of the muscle (Fig. 18); when abducted, however, the nerve lies horizontally, although laterad to the muscle. It is hypothesised that the unusual position of the nerve is due to the reorientation of muscle A_1i to the outer face of the lower jaw. I thus consider that the inner element of A_1 having its origin from the quadrate is homologous in the Kneriidae and Phractolaemidae.

Within the Kneriidae, muscle A_1i originates from the mid-lateral ledge or the quadrate (*Cromeria*) or its lateral anterior face (*Kneria* and *Parakneria*). In the Phractolaemidae the origin of the muscle is from a lateral quadrate spine. The lateral quadrate origin of muscle A_1i in kneriid genera is taken to be synapomorphic and is supported by other synapomorphies noted above, *viz*: laterally extended mesethmoid wings, nodular mesethmoid rostral process, ventrally inclined and rostrally extended vomer, and reduction of branchiostegal ray number (to 3). The characters listed by Lenglet (1974:95) as separating the genera *Kneria* and *Parakneria* appear ones of degree and on the basis of synapomorphies of the skeleton and jaw musculature, the two genera should probably be considered as a single genus, *Kneria,* which forms the sister-group to *Cromeria.*

Grasseichthys is characterised myologically by reduced adductor and suspensorial muscles. Only a single *adductor mandibulae* element has been identified whilst an *adductor arcus palatini* muscle appears to be absent. *Grasseichthys* was considered by Géry (1964) to belong to a separate family, but was included in the Kneriidae by Greenwood *et al.* (1966). Such a placement appears to be the correct procedure since *Grasseichthys* shares with other kneriids a reduced opercular aperture (see p. 291) and similar ethmoid morphology (laterally extended mesethmoid wings and nodular rostral process). Both an ectopterygoid and metapterygoid appear to be lacking in the specimen of *Grasseichthys* to hand; the sympletic is elongate rather than short as in other kneriids. Branchiostegal rays are reduced to two.

No myological characters support Patterson's (1984a) placement of the Gonorynchidae as the sister-group to the Kneriidae. A single 'loss' character, *viz.* absence of muscle A_w, is shared by the Gonorynchidae, Kneriidae and Phractolaemidae (the muscle is also absent in various otophysan taxa and its absence can hardly be considered a 'strong' synapomorphy). The Gonorynchidae and Phractolaemidae share a divided A_2 muscle where in *Phractolaemus* the dorsal division inserts on the antorbital and in *Gonorynchus* on the lachrymal. In both taxa the ramus mandibularis of the V nerve runs anterior to the division of A_2.

In addition to the derived adductor musculature, the Phractolaemidae shares with the Kneriidae (including *Grasseichthys*) anteriorly extended lateral ethmoid wings (see Thys van den Audenaerde, 1961, fig. 15), reduction of branchiostegal ray number to a single element, *cf* 2 or 3 in kneriids, 4 or 5 in *Gonorynchus* and *Chanos* and partial sealing of the opercular border to the body wall.

Scale morphology

Fink & Fink (1981) suggest a close relationship between *Kneria* and *Gonorynchus* based on a derived scale pattern, this pattern being one of parallel longitudinal striae, and with circuli restricted to the scale margins. In fact the scale morphology of *Chanos, Gonorynchus, Kneria-Parakneria* and *Phractolaemus* differs quite markedly. Whilst circuli are restricted to the borders of the scales in *Gonorynchus* and kneriids, the longuitudinal striae display different patterns. In *Gonorynchus* the striae are divergent, but both parallel and divergent in the kneriids. This latter feature varies too according to the part of the body on which the scales are situated. Moreover, the scales of the kneriids bear more deeply incised striae which have a wavy appearance (Fig. 22D). The scales of *Gonorynchus* have markedly ctenoid anterior and posterior margins (Fig. 22A and Le Danois, 1966: 286 & fig. 2). In overall shape the scales of *Phractolaemus* and *Chanos* resemble one another closely, but this is in a symplesiomorphic sense, the scales being typically rounded with close-set concentric circuli on the posterior field and many radial striae on the anterior field (Figs 22B & C). Both *Cromeria* and *Grasseichthys* lack scales. The variance in scale morphology within the gonorynchiforms appears to make it an unrewarding character for assessing phylogenetic relationships.
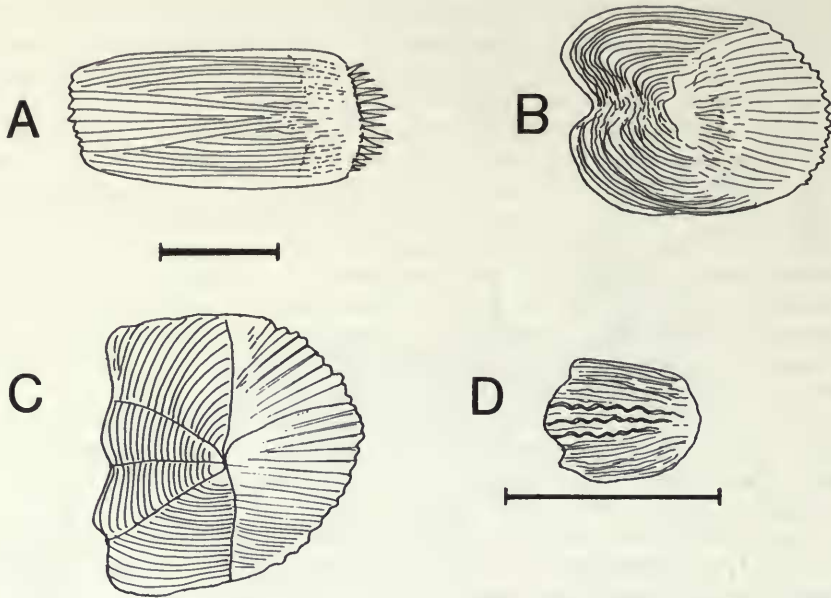
Fig. 22 Body scales of gonorynchiform genera: A, *Gonorynchus gonorynchus*; B, *Chanos chanos*; C, *Phractolaemus ansorgei*; D, *Kneria auriculatus*. All taken from the mid-flank below the lateral line. Scale = 1 mm.

Epibranchial organ

The structure of the epibranchial organ in gonorynchiforms deserves some comment. Nelson (1967) has claimed that epibranchial organs in various groups of lower euteleosts (Osteoglossiformes, Cypriniformes, Clupeiformes, Gonorynchiformes and argentinoids) have been independently derived in those lineages. That this is so, appears to be evident from the nature of the involvement of various elements of the posterior upper and lower gill-arches, and in the overall structure of the organ itself (see Nelson, 1967). In gonorynchiforms both the 4th and 5th epibranchials are supporting elements of the investing diverticulum. The 5th epibranchial is a well-developed cartilaginous element in all gonorynchiform taxa and bears gill-rakers. In *Chanos,* the epibranchial organ is a highly developed structure with each diverticulum in the form of a medially recurved, finger-like sac (see Kapoor, 1954). The 4th epibranchial is a stick-like bone with a high dorsal process; the 5th epibranchial is a broad, bifurcated element (Nelson, 1967, fig. 1j).

In other gonorynchiform genera, the epibranchial diverticulum is not recurved as in *Chanos,* but is a straight, finger-like sac projecting antero-medially. In *Gonorynchus* the 4th epibranchial is a massive element and the 5th a slender curved, rod-like cartilage (Fig. 9).

In *Kneria* and *Parakneria* there is, posterior to the junction of the 4th epi- and ceratobranchials, a curved cartilaginous element that I take to be the 5th epibranchial. The diverticulum is cone-shaped and invests the 4th and 5th ceratobranchials, but not the 5th epibranchials (Fig. 15).

In *Cromeria* there is a 5th epibranchial (labelled by d'Aubenton, 1961, as an accessory epibranchial). It is not clear from my specimens as to which elements the epibranchial pouch covers, but the situation appears like that in *Kneria* with the 4th epibranchial providing little contribution to the support of the diverticulum. There is an ossified 5th basibranchial, a feature shared with other kneriids.

In *Grasseichthys* the diverticulum of the organ is not well-developed and only a few gill-rakers are present in the pouch. Greenwood *et al.* (1966) figured the gill-arches of *Grasseichthys* but they did not show a 5th epibranchial, which occurs as a small cartilage postero-dorsal to the 4th

epibranchial. The 4th epibranchial has an elongate dorsal process and the bone appears to contribute to the support of the diverticulum.

In *Phractolaemus* the cartilaginous tips of the 4th and 5th ceratobranchials are in contact; the diverticulum involves only the 4th and 5th ceratobranchials.

In all taxa the epibranchial diverticula communicate directly with the oesophagus and appear to incorporate fibres of the *sphincter oesophagi* muscle (see d'Aubenton, 1961; Thys van den Audenaerde, 1961). Also, the diverticula appear attached to the *posterior transversi dorsales* muscles.

In summary, the epibranchial organ seems most highly developed in *Chanos* (see Kapoor, 1954); amongst gonorynchoids, the Kneriidae and Phractolaemidae differ from the Gonorynchidae in the degree of association of the epibranchial diverticulum with the posterior gill-arch elements; the 4th epibranchial contributing no or little support to that structure in the former two families.

To summarise the results of this study:

1. *Chanos* has a basically plesiomorphic jaw, hyoid and suspensorial muscle arrangement. It shares with *Gonorynchus* a divided A_1 muscle where part inserts on the lower jaw. This is probably a plesiomorphic condition for gonorynchiforms.

2. *Gonorynchus* has several jaw and suspensorial muscle autapomorphies (p. 283). Regrettably, no conclusive synapomorphies have been identified that would corroborate the pattern of relationships hypothesised by Fink & Fink (1981) and Patterson (1984*a*), that *Gonorynchus* is the sister-group to the Kneriidae.

3. *Phractolaemus* has several jaw muscle apomorphies one of which, a divided A_2 it shares with *Gonorynchus* (see p. 299). With *Cromeria, Kneria* and *Parakneria* it shares a divided A_1 of which part originates from the quadrate; anteriorly extended lateral ethmoid wings and reduced number of branchiostegal rays. *Phractolaemus* has a specialised swimbladder and pulmonary system enabling it to utilise atmospheric air (see Thys van den Audenaerde, 1961). *Kneria,* also, is apparently capable of atmospheric respiration (see discussion in Lenglet, 1973 and observations of Bell-Cross 1976:97) and this may represent another synapomorphy.

4. *Kneria, Parakneria* and *Cromeria* possess a synapomorphic arrangement of *adductor mandibulae* muscles (p. 291) in addition to sharing derived ethmo-vomerine morphologies (p. 293). There seems little doubt that they represent a monophyletic unit.

5. *Grasseichthys* has a autapomorphically reduced jaw muscle system. It shares with *Kneria, Parakneria* and *Cromeria* a derived ethmo-vomerine morphology, reduced number of branchiostegal rays and partially sealed operculum (the two latter characters shared also with *Phractolaemus*, see p. 299). *Grasseichthys* shares with *Phractolaemus* an elongate, spine-like interoperculum, and with *Cromeria,* the absence of body scales.

From these data the Phractolaemidae and Kneriidae appear to be related as sister groups (this is on the assumption that, in the light of other synapomorphies listed here and given in Fink & Fink, 1981 and Patterson, 1984*a*, that the divided A_2 muscle present in the Phractolaemidae and Gonorynchidae is homoplasious).

Grasseichthys which is currently assigned to the Kneriidae, lacks those myological features identified as synapomorphic for the other kneriids, although it shares derived osteological features with them (see above). There is, however, a character conflict in that *Grasseichthys* shares with *Phractolaemus* a derived interopercular morphology (p. 294), and it may also be that the single adductor muscle is homologous with the dorsolateral division (A_2o) of *Phractolaemus* (p. 295). It is not therefore possible on present evidence to determine whether it is more closely related to the kneriid or phractolaemid lineage.

Both *Cromeria* and *Grasseichthys* have been regarded by some authors as neotenic, or paedomorphic (see D'Aubenton, 1961; Lenglet, 1974), presumably because of a general lack of skeletal ossification, 'larval appearance' and miniature size (see Roberts, 1984 for a list of neotenic features pertaining to salangoids, but common to other groups). If indeed these taxa are paedomorphic, then *Grasseichthys* might well be viewed as representing an ontogenetic stage

where the adductor musculature, rather than being 'reduced' is merely retarded in its development, as might also be the 'loss' of scales in both *Grasseichthys* and *Cromeria*.

Whether paedomorphosis (by retardation) alone is the mechanism responsible for dwarfed lineages is discussed by Hanken (1984). Hanken argues that 'Parallel morphological evolution in related groups may be explained as a consequence of their sharing common developmental pathways which are truncated in an analagous manner, albeit independently. In the case of closely related taxa, parallelism may even be *expected*'. However, if two groups are known to be closely related, presumably on the basis of shared homologies (synapomorphies) then why should 'parallel morphological evolution' be evoked? The 'common developmental pathways' must also be synapomorphic. Should the epigenetic cause(s) of truncation in related taxa be the same, then, presumably the resulting paedomorphosis must be regarded as synapomorphic.

Another of Hanken's assertions is that decreased body size is associated with 'morphological novelty'. Granted, truncation of development will be at different stages in each group but these terminal stages will simply be autapomorphic, characterising each taxon. Thus, it is difficult to see how paedomorphic taxa are susceptible to any greater degree of 'morphological novelty' than those taxa whose ontogeny has 'deviated' in some other way from the plesiomorphic pattern of development.

Acknowledgements

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